Macrofaunal communities associated to free-living bladderwrack *Fucus vesiculosus* (L.)

Photo by Roxana Preston

Viivi Halonen

Master's thesis

Ecology and Evolutionary Biology

Faculty of Biological and Environmental Sciences

University of Helsinki

May 2021

HELSINGIN YLIOPISTO
HELSINGFORS UNIVERSITET
UNIVERSITY OF HELSINKI

Tiivistelmä

Tiedekunta: Bio- ja ympäristötieteellinen

Koulutusohjelma: Ekologian ja evoluutiobiologian maisteriohjelma

Opintosuunta: Ekologia ja evoluutiobiologia

Tekijä: Viivi Halonen

Työn nimi: Vapaana elävän rakkohaurun *Fucus vesiculosus* (L.) eliöyhteisöt

Työn laji: Maisterintutkielma

Kuukausi ja vuosi: Toukokuu 2021

Sivumäärä: 45

Avainsanat: vapaana elävä, makrolevä, rakkohauru, *Fucus vesiculosus*, Itämeri, macrofauna, makroinfauna, makroepifauna, eliöyhteisö

Ohjaaja tai ohjaajat: Iván Franco Rodil, Roxana Preston

Säilytyspaikka: HELDA - Helsingin yliopiston digitaalinen arkisto / HELDA - Helsingfors universitets digitala publikationsarkiv /HELDA - Digital Repository of the University of Helsinki

Muita tietoja:

Tiivistelmä:

Yksi Itämeren avainlajeista, rakkohauru *Fucus vesiculosus* on viime vuosisadan aikana vähentynyt ihmisen toiminnan vaikutuksen takia. Rakkohaurun tavallista muotoa, joka elää kiinnittyneenä koviin pintoihin, uhkaa tulevan vuosisadan aikana rehevöityminen sekä muutokset veden lämpötilassa ja suolapitoisuudessa. Rakkohaurua tavataan Itämeressä myös harvinaisempana vapaana elävänä muotona, joka elää ajelehtien matalissa ja suojaisissa poukamissa. Vapaana elävää rakkohaurua on tutkittu hyvin vähän eikä sen roolia ekosysteemissä tai mahdollisen häviämisen seurauksia tunneta. Vapaana elävä muoto on mahdollisesti kiinnittynyttä muotoakin alttiimpi rehevöitymisen seurauksille. Tämän lisäksi vielä ei tiedetä aiheuttaako vapaana elävä rakkohauru sedimentin hapettomuutta leväkerroksen alla. Tässä opinnäytetyössä selvitän vapaana elävän rakkohaurun makroepifauna- ja makroinfaunayhteisöt useassa näytteenottopaikassa sekä Suomessa että Ruotsissa. Arvioin myös aiheuttaako rakkohaurun läsnäolo sedimentin hapettomuutta.

Tutkimukseen kerättiin replikaatteja sekä rakkohaurukasvustosta sekä sedimentistä rakkohaurun alta ja läheiseltä paljaalta merenpohjalta. Kaikki selkärangattomat tunnistettiin, laskettiin ja punnittiin. Jokainen rakkohaurureplikaatti punnittiin sekä kasvuston korkeus mitattiin.

Tutkimus osoitti, että vapaana elävän rakkohaurun läsnäololla on eliöyhteisöön samanlainen vaikutus näytteenottopaikasta ja maasta riippumatta. Tuloksista ilmeni myös, että rakkohaurun märkäpainon kasvaessa epifaunan eliörunsaus sekä biomassa kasvoivat. Tutkimuksen suurimmat eliörunsaudet sekä biomassa löytyivät kahdelta näytteenottopaikalta paljaalta sedimentiltä, joiden eliöyhteisöt koostuivat pääasiassa opportunistisista taksoneista. Tulokset mahdollisesti osoittavat ettei vapaana elävä rakkohauru aiheuta sedimentin hapettomuutta.

Tämä tutkimus oli ensimmäinen katsaus vapaana elävän rakkohaurun eliöyhteisöön. Tutkimus osoitti että vapaana elävä rakkohauru on mahdollinen avainlaji Itämeren suojaisissa ja matalissa poukamissa. Rakkohaurun läsnäolo lisäsi paikalla olevan lajiston määrää verrattuna lähellä olevaan paljaaseen merenpohjaan. Epifaunayhteisö hyötyi suuremmasta rakkohaurun biomassasta, eikä rakkohaurulla havaittu olevan negatiivisia vaikutuksia infaunaan.

HELSINGIN YLIOPISTO
HELSINGFORS UNIVERSITET
UNIVERSITY OF HELSINKI

Abstract

Faculty: Biological and Environmental Sciences

Degree programme: Master's programme in Ecology and Evolutionary Biology

Subject/Study track: Ecology and Evolutionary Biology

Author: Viivi Halonen

Title: Macrofaunal communities associated to free-living bladderwrack *Fucus vesiculosus* (L.)

Level: Master's thesis

Month and year: May 2021

Number of pages: 45

Keywords: free-living, unattached, macroalgae, *Fucus vesiculosus*, Baltic Sea, associated, macrofauna, macroinfauna, macroepifauna

Supervisor or supervisors: Iván Franco Rodil, Roxana Preston

Where deposited: HELDA - Helsingin yliopiston digitaalinen arkisto / HELDA - Helsingfors universitets digitala publikationsarkiv /HELDA - Digital Repository of the University of Helsinki

Additional information:

Abstract:

During the last century, a decline in the canopy-forming foundation species *Fucus vesiculosus* has been observed in the Baltic Sea. The widely studied typical form of *F. vesiculosus*, that lives anchored to hard substrata, is at risk of further declines in the following century due to eutrophication and changes in water temperature and salinity. *Fucus vesiculosus* also exists in the Baltic Sea as a less common free-living form, which lives deposited in sheltered and shallow bays. This free-living form has been left understudied and little is known about their role in the ecosystem or the potential consequences of its disappearance. However, their occurrence may be equally or more under threat in the event of the aforementioned environmental changes. Additionally, it is currently unknown if mats of *F. vesiculosus* cause anoxia in the sediment below. This thesis will investigate the macroepifaunal and macroinfaunal communities associated to the presence of free-living *F. vesiculosus* across different sites in both Finland and Sweden. We will also estimate if *F. vesiculosus* causes anoxia.

For this study, replicate frames of *F. vesiculosus*, including all vegetation and epifaunal community, were collected using mesh bags. Infaunal samples were randomly collected using benthic cores, both under the mat of *F. vesiculosus* and the adjacent bare soft bottom. All macroinvertebrates were identified to the lowest possible taxa, counted and weighed. Morphological measurements of *F. vesiculosus* thalli, such as length of thallus and wet weight, were recorded for every frame.

Our results showed that the presence of free-living *F. vesiculosus* has a consistent effect across the two study locations. We found that increasing wet weight of *F. vesiculosus* significantly increased the abundance and biomass of the macroepifauna. The highest infaunal animal abundance and biomass were found in the bare sediment with high occurrence of opportunistic taxa. However, we found potential evidence to suggest that the presence of *F. vesiculosus* mats does not cause anoxia in the sediment.

This study provides a much-needed first look into the macrofaunal communities associated to the free-living *Fucus vesiculosus*. Our study demonstrated that free-living *F. vesiculosus* is a potential foundation species in shallow, sheltered bays of the Baltic Sea by increasing the number of present taxa compared to adjacent bare sediment. Higher *F. vesiculosus* biomass directly increased the abundance and biomass of the macroepifaunal community, and the presence of free-living *Fucus vesiculosus* was not found to have significant negative effects on the associated macroinfaunal community.

Table of Contents

1. Introduction

1.1. Coastal vegetation

The majority of the biodiversity in large water bodies, such as seas and oceans, is concentrated in relatively narrow areas close to the coastline. In these habitats, stable and long-term habitat-forming organisms, such as corals, oysters, salt marsh grasses and macroalgae, add a level of spatial complexity to an otherwise morphologically simple substrate and can modify a wide range of physical and environmental factors (Pandolfi et al 2003, Krumhansl et al 2006, Gedan & Bertness 2010, Beck et al 2011). These organisms can, for example, provide food and shelter in areas where they would otherwise be lacking, thus enhancing local species richness and abundance; contributing greatly to local biodiversity (Irigoyen et al 2011). Habitat-forming organisms are often referred to as foundation species due to their capacity of allowing a multitude of other organisms to live and thrive in their vicinity. The ecosystem services provided by foundation species are highly valuable, with coastal vegetation such as kelp forests (order *Laminariales*) alone being estimated in the range of billions of dollars annually (Krumhansl et al 2006).

In coastal rocky shores lacking soft substrate for vascular plants to grow, the role of macrophyte foundation species is occupied by macroalgae. Macroalgae are a polyphyletic group consisting of three taxa: the green algae (*Chlorophyta*), the red algae (*Rhodophyta*) and the brown algae (*Phaeophyta*). Macroalgae have evolved in aquatic environments, distinguishing them from aquatic plants which evolved from ancestors living on land. The only marine angiosperms living a fully submerged life are seagrasses, such as *Zostera* spp (Olsen et al 2016).

Higher plants have a vascular system resembling a bloodstream, which transports water and nutrients from roots to the other parts of the organism, while transporting photosynthetic products from leaves to the other parts of the plant. In algae, photosynthesis occurs over the entire organisms, and the whole algae body can uptake nutrients and water. Algae have parts resembling roots, holdfasts, which are only used to attach to substrata. Thus, aquatic plants are generally encountered in areas with soft sea bottom, whereas macroalgae are common in rocky areas.

Perennial, canopy-forming macroalgae, such as the brown algae kelp, create locally stable conditions for other species in the community by increasing habitat complexity and providing shelter and foraging opportunities to a wide array of organisms (Miller et al 2015). Macroalgae contribute to the stability of ecosystem functioning and provide numerous ecosystem services, including shoreline protection, nutrient cycling and sheltering and feeding many commercial and non-commercial fisheries (Krumhansl et al 2006). For instance, kelps create subtidal forests that can alter light, nutrient, and

hydrodynamic conditions in addition of modifying larval recruitment patterns, while simultaneously providing food and shelter for a diversity of fauna (Metzger et al 2019).

The productivity of macroalgae as primary producers is astonishing, with kelp productivity rivalling that of tropical rainforests or intense agricultural lands (Krumhansl et al 2006). Not only does this productivity create abundant food resources and large surface areas to reside upon for grazers living on the algae, but macroalgae are a source of organic matter for the surrounding area and deeper sea floor when algae detach and get transported away (Takolander 2018, Attard et al 2019).

In recent decades, ongoing population declines have been observed in coastal habitats formed by corals, shellfish, seagrasses and kelps (Pandolfi et al 2003, Krumhansl et al 2006, Beck et al 2011, Olsen et al 2016). All these habitats provide substantial ecosystem services valuable to humankind, and the loss of these species may have devastating consequences to human well-being (Grabowski et al 2012, Vásquez et al 2014, Woodhead et al 2019). Even the historical resilience of kelp forests has a limit, and their ability to recover from environmental disturbance might be deteriorating. Several faunal species are positively associated with kelp forests, and biodiversity will change substantially if kelp is absent (Bodkin 1988, Miller et al 2015).

During the last century, a decline in canopy-forming foundation species has been observed in the Baltic Sea as well, notably in the brown algae *Fucus vesiculosus* (L.). The typical form, attached to hard substrata, has been demonstrated to be at risk of further declines in the following century due to eutrophication and changes in water temperature and salinity (Takolander 2018). The less common free-living form has been less studied, but its occurrence may be equally or more under threat in the event of aforementioned environmental changes. Free-living *Fucus vesiculosus*, formed of detached living algal thalli deposited in soft sea bottoms, has been left understudied, and thus its role in the ecosystem and consequences of its disappearance are unknown. This thesis will tackle this subject by investigating the faunal community, both infaunal and epifaunal, associated to the presence of free-living *Fucus vesiculosus* in both Finland and Sweden.

1.2. The Baltic Sea

Formed 13 000 years ago, the Baltic Sea stands as the youngest regional sea of the northern hemisphere. The waters of the unique, atidal Baltic Sea are characterized by a salinity gradient of brackish water, with about 20 PPT (Parts Per Thousand) at Kattegat between the Swedish and Danish coast and almost freshwater in the northernmost Gulf of Bothnia (Figure 1). Due to its young age and brackish nature, the Baltic Sea has only been colonized by a relatively small number of species. The species community structure shifts from mostly of marine origin towards a freshwater origin in the

north. Because of this low species diversity, the Baltic Sea ecosystem is constantly at risk of fast environmental deterioration and the loss of crucial ecosystem services.

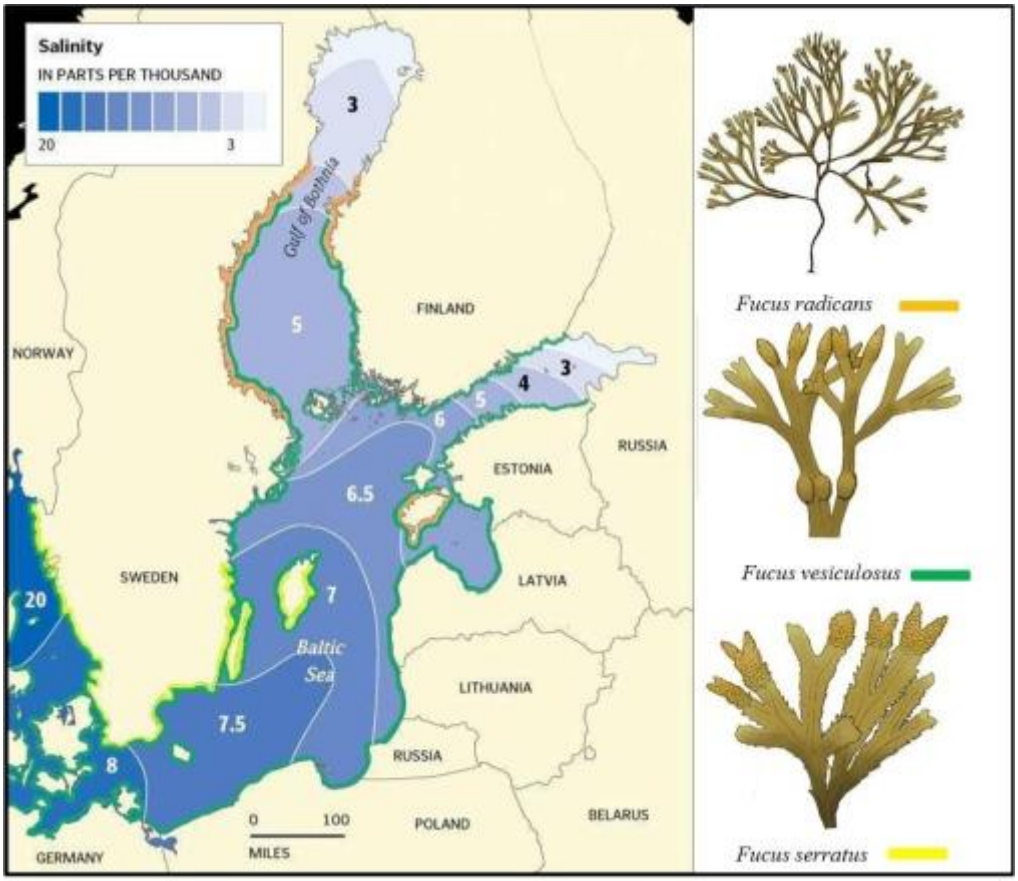


Figure 1. Map of the Baltic Sea, showing the surface water salinity gradient (indicated in PPT, Parts Per Thousand) and the species distribution of the three algae of the genus *Fucus* found in the Baltic. Green: Bladderwrack (*Fucus vesiculosus*); orange: narrow wrack (*Fucus radicans*); yellow: serrated wrack (*Fucus serratus*). Image source: DEEP (2015), accessed on 26/04/2021.

With an average depth of 55 metres, the Baltic Sea is relatively shallow with a small water volume, which makes its waters especially vulnerable to warming. The Baltic Sea has the highest documented warming rate of the large marine ecosystems of the world, with an observed warming 3-7 times higher than the global average during the last 30 years (Belkin 2009). Consequently, the frequency of extreme temperatures has been increasing as well. Future projections predict further increases in the sea surface temperature, with an average increase of 2-3 °C by the end of the century (Meier 2006).

Furthermore, over 85 million people live on the drainage area of the Baltic Sea (HELCOM 2018). This is one contributing factor as to why the Baltic Sea is one of the seas most affected by modern anthropogenic activity. During the last century, the consequences of overfishing, habitat loss, climate change and eutrophication have become increasingly evident (Bonsdorff et al 1997). Anthropogenic activity has also brought multiple alien species to the region, which represent a threat or a potential threat to the small local species community (Leppäkoski et al 2002).

1.3. Coastal vegetation of the Baltic Sea

In the northern Baltic Sea, the macroalgal community consists of both annual, filamentous algae and a few large perennial species, such as *Fucus* spp. (Figure 1). The perennial species of the Baltic Sea have high ecological importance, as they provide a stable habitat and an overwintering structure as well as a food source for numerous smaller organisms (Torres et al 2015).

The algae in the rocky littoral zone of the Baltic Sea follow a general zonation pattern. The upper rocky shore, scraped bare by sea ice during winter, is occupied during the summer by annual, filamentous algae. Below the filamentous algae resides a belt of perennial macroalgae, such as *Fucus vesiculosus*. Below the layer of *Fucus* spp. live algae capable of photosynthesis in low light conditions, such as red algae (Kiirikki 1996).

In the Baltic Sea, studies on coastal vegetation have focused mainly on eelgrass *Zostera marina* (Boström & Bonsdorff 1997, Baden et al 2003, Boström et al 2014) and the attached form of bladderwrack *Fucus vesiculosus* (Korpinen et al 2010, Kersen et al 2011, Takolander 2018, Rodil et al 2020). Their associated faunal communities have been well documented and data exists on temporal changes of the communities and their interactions (Korpinen et al 2010, Kotta et al 2019, Rodil et al 2020). The risks of anthropogenic activities have been investigated as well, with predicted increasing temperatures and decreasing salinity levels being the most prominent threats alongside eutrophication (Takolander 2018).

1.3.1. Fucus vesiculosus

Three perennial species of the genus *Fucus* are encountered in the Baltic Sea (Figure 1). One of them, *Fucus radicans* (Bergström & Kautsky), is a species endemic to the Baltic Sea, described in 2005 (Bergström et al 2005). The second Fucoid species of the Baltic Sea is the serrated wrack *Fucus serratus*, of which observational data exists only from the southern Swedish coast, at the lowest salinities of 7 PPT (Figure 1). The most widespread of them is bladderwrack *Fucus vesiculosus*, which is found in most of the Baltic Sea except the northern Bothnian Bay and eastern Gulf of Finland (Figure 1).

The bladderwrack *Fucus vesiculosus* (hereafter *Fucus*) is a perennial, canopy-forming fucoid brown algae (Phaeophycae) that can form large monospecific underwater forests in the Baltic Sea. Similarly to Laminariales in temperate and polar coastlines throughout the northern hemisphere, underwater *Fucus* forests provide important ecosystem functions and services within the Baltic Sea. As an important foundation species, stands of *Fucus* provide a habitat and/or a food source to a wide array of animals, notably several species of fish and macroinvertebrates (Wikström and Kautsky 2006, Nohrén and Odelgård 2010). Moreover, *Fucus*-bed communities have high oxygen production rates

and are a source of organic matter as algal detritus for habitats adjacent to the canopy (Attard et al 2019).

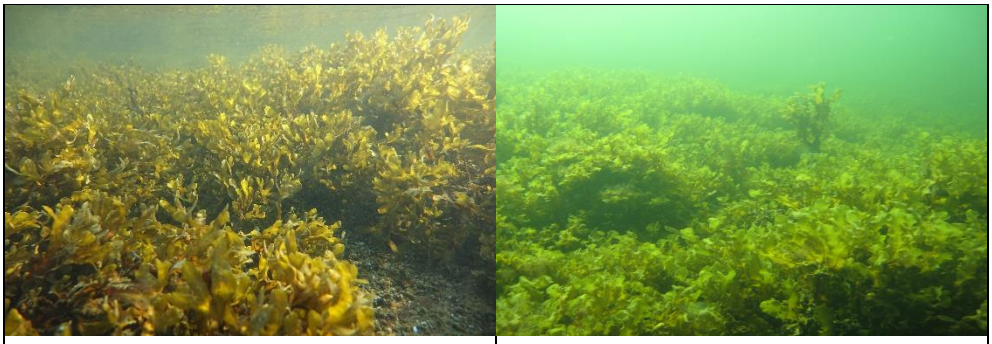
Fucus colonized the Baltic Sea from the Atlantic Ocean 8000 years ago (Pereyra et al 2013). The originally intertidal species lives a completely submerged lifestyle in the Baltic Sea, due to the latter's atidal nature. *Fucus* forms a belt under the waterline below a littoral layer comprised of annual, filamentous algae that live close to the surface. *Fucus* is characterized by a frond with a prominent midrib and spherical air bladders that are often paired. It lives on rocky shores attached via a holdfast and commonly reaches sizes of 20-40 cm in the Baltic Sea (Forslund et al 2012).

1.3.2. Morphological types of Fucus

Fucus can be found as three types in the Baltic Sea: (1) the typical attached morph that is anchored to hard substrata via a holdfast, (2) the decomposing drift algae originating from attached *Fucus* torn off its substrata and (3) the unattached free-living morph that lacks a holdfast and lives deposited in shallow sheltered sea bottoms (Figure 2, A+B) (Svedelius 1901, HELCOM 2013). Communities of free-living *Fucus* are formed when attached *Fucus* is torn off its substratum and drifts into a sheltered bay, where it may continue its life instead of dying and decomposing (Svedelius 1901, Häyrén 1949, Bauch 1954, Luther 1981). When torn, *Fucus* is rarely able to form a new holdfast, but it can live without one, lying on shallow soft sediments.

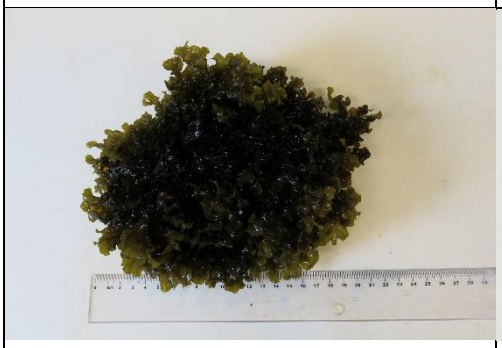
Communities of free-living *Fucus* are formed when attached *Fucus* is torn off its substratum and drifts into a sheltered bay, where favourable environmental conditions may allow it to continue living. When torn, *Fucus* is sometimes able to form a new holdfast in the Baltic Sea although this is rare (Tatarenkov et al 2005). *Fucus* is able to form new free-living populations via fragmentation in sheltered bays.

The morphology of *Fucus* varies widely depending on the environmental conditions of its habitat. Fucoid species can exhibit phenotypic plasticity in response to various abiotic factors such as light intensity, extreme temperatures, and tidal exposure (Brinkhuis and Jones 1976). The morphology of the attached morph is affected by exposure to waves and salinity (Ruuskanen and Bäck 1999). The free-living morph also exists as several different forms, ranging from 'typical-size' to 'dwarf-size' forms (Figure 2, C+D) (Kjellman, 1890; Svedelius, 1901; Waern, 1952; Luther, 1981).



A.

B.



C.

D.

Figure 2: (A) Habitat of attached morph of *Fucus vesiculosus*, Tvärminne Zoological Station. (B) Habitat of unattached morph of *F. vesiculosus*, Askö Laboratory. (C) Typical-size form of free-living *F. vesiculosus*. (D) Dwarf form of free-living *F. vesiculosus*.

A Photo by Karl Attard, B Photo by Ellen Schagerström, C+D Photos by Roxana Preston.

Free-living *Fucus* has been documented historically from coastal bays and lagoons in several countries along the shore of the Baltic Sea. These include Sweden, Finland, Germany, Estonia and Poland, but the free-living morph has disappeared from Poland since the 1950s due to eutrophication (HELCOM 2013). All habitats characterized by the presence of the dwarf type of the free-living morph have been classified as endangered by HELCOM Red List (2013). The habitats are threatened by eutrophication and related phenomena, namely decreasing light penetration depth, increasing growth of filamentous algae and higher sedimentation rate (HELCOM 2013).

Although the functional role and the associated macrofaunal communities of *Fucus* in rocky bed communities have been previously documented (Korpinen et al 2010, Kersen et al 2011), the free-living lifestyle has received less attention.

1.4. Anthropogenic impacts on *Fucus*

Anthropogenic activity has globally altered the function of ecosystems and climate, which will be continuing to change in the foreseeable future as well. In the Baltic Sea, the most notable

consequences of anthropogenic activity are eutrophication and climate change, the latter is predicted to affect at least water temperature and water salinity levels (Meier 2006).

Historically, anthropogenic activity has deteriorated stands of *Fucus* in Finland, among others. An extensive decline of *Fucus* belts occurred in South-Western Finland during the late 1970s, disappearing almost completely from some shores (Kauppila & Bäck 2001). It has since recolonized its former distribution areas only in the upper littoral, being continuously present only at depths of 1-4 m, a mere shadow of *Fucus* belts reaching below 10m in the early 20th century (Kauppila & Bäck 2001).

1.4.1. Eutrophication

The legacy of eutrophication is a big issue in the Baltic Sea, a relatively small and shallow water body. Waste waters and intensive agriculture flush excessive nutrients into the Baltic Sea, which favours filamentous algal species that thrive from the increased nutrients, as opposed to larger and fleshy algae (Kiirikki & Blomster 1996). As both attached and unattached filamentous algae can have a fast growth rate, eutrophication has multiplied their occurrences and they tend to overgrow on the surface of perennial macrophytes (Bonsdorff et al 1997). Overgrowth on epiphytes limits the light available to the host plant and causes drag in the water flow among other effects, which have caused *Fucus* abundances to decline in recent decades (Berger et al 2003).

Eutrophication has also led to a decrease of the euphotic zone due to reduced available light in the water body (Kautsky et al 1986). Increased nutrients have stimulated the growth of phytoplankton, which in turn increase water turbidity. Due to a combined effect of turbidity and overshadowing by epiphyte growth, *Fucus* is unable to grow as deep as before since light does not reach the same depths as it historically has. For instance, the illuminated seafloor of Archipelago Sea has decreased by half from 1930 to 2007 (Tolvanen et al 2013). The increased turbidity has an additional consequence of faster sedimentation rate which especially affects macroalgae growing in sheltered areas, such as free-living *Fucus.* Eutrophication has already caused the free-living morph to disappear from Poland (HELCOM 2013). All these factors have consequentially shifted the *Fucus* belt toward the surface during the last century, which reduces the *Fucus* biomass as well (Kautsky et al. 1986, Torn et al 2006, Rohde et al 2008).

1.4.2. Elevated water temperature

Water temperature has an important implication on the species distribution of algae, as species-specific temperature tolerances dictate the rates of growth and photosynthesis (Takolander et al 2017b). For instance, Takolander et al (2017b) discovered that attached *Fucus* is vulnerable to short periods of high temperatures (26-28 ^{o}C for 8 days), which caused decline in the growth rate of the algae and induced varying levels of tissue necrosis.

The predicted increase of the water temperature and recurring temperature extremes by the end of the 21st century will have considerable implications on the species distribution of the Baltic Sea we know today. The environmental tolerance of several species living the Baltic Sea is already at their limit in the current climate, and the range of these species may see a major shift towards the south with increasing extreme events such as heat waves combined with decreasing salinity (Roth et al 2010, Takolander et al 2017b). The southward shift of foundation species will have a significant effect to the biota linked to its presence, which will have to shift their range along with their host (Takolander et al 2017a).

1.4.3. Decreased salinity

The occurrence threshold of the most tolerant macroalgae of marine origin within the Baltic Sea is around salinities 3-4 PPT (Takolander 2018). It is predicted that this limit will be shifting towards the south by the end of the century, due to increased precipitation rates and the decreasing frequency of salt pulses from the Danish straits (Meier 2006). Lower salinity decreases the growth rate of *Fucus* causing it to be outcompeted by faster growing species, which will likely cause the distribution of *Fucus* to shift towards the south of Baltic Sea (Takolander 2018). Additionally, low salinity amplifies the negative effects of high temperatures, and the synergy of these environmental changes may cause an even stronger reaction in the distribution of *Fucus* than either change alone (Takolander et al 2017b).

1.5. Relevance of the study, aims and hypotheses

Aquatic vegetation influences the spatial distribution of associated fauna by providing habitats and substrates for the epifaunal and infaunal communities as well as affecting predator-prey relationships by increasing habitat complexity (Boström & Bonsdorff 1997, Duffy 2006, Christie et al 2009). For instance, the disappearance of attached *Fucus* had a negative effect on the biomass and abundance of invertebrate species, with animal biomass dropping to about half of the animal biomass of sites with present *Fucus* (Wikström & Kautsky 2007).

1.5.1. Relevance of the study

Changing abiotic conditions, namely eutrophication and changes in temperature and salinity, pose a threat to the current distribution of the attached lifestyle of *Fucus* in the Baltic Sea. Eutrophication and related phenomena are established threats to the free-living morph as well, as its habitat (shallow and sheltered bays) is at high risk of future warming. Increasing temperatures combined with decreasing salinity levels may put free-living *Fucus* under considerable environmental pressure during the following century.

Understanding the variability of the macrofaunal community associated to free-living *Fucus* is crucial to understand the ecological role of the free-living morph in coastal environments. Macroinvertebrate

benthic fauna provide a multitude of important ecological services that help counteract the effects of eutrophication (Karlson et al 2007). Macrofaunal activity in the sediment impacts biogeochemistry through bioturbation, by allowing oxygen to penetrate deeper sediment layers and by affecting nutrient fluxes (Karlson et al 2007, Gammal et al 2017). Many benthic invertebrates are also an important food source for several species of both commercial and non-commercial fish (Florin & Lavados 2010, Jakubavičiūtė et al 2017), thus understanding the function and structure of benthic invertebrate communities is both ecologically and economically necessary.

HELCOM (2013) estimated that high abundances of free-living *Fucus* may induce anoxia in the sediment layer below, which can cause fauna living in the sediment under *Fucus* to die. However, to our knowledge this has not been investigated before and the true impact of free-living *Fucus* on infauna is unknown.

1.5.2. Study aims

Little is known about the ecological role of free-living *Fucus* (Meyer et al 2019, Austin et al 2021). The focus of this thesis was to document the macrofaunal community associated to free-living *Fucus* and to estimate the effect of its presence on the macroepifaunal and macroinfaunal communities. We will compare the community of *Fucus* to the community of adjacent bare soft bottom benthic habitats to assess the effect of *Fucus* on infauna and estimate whether the conditions under *Fucus* are anoxic. Additionally, we will test the spatial resolution of the effects of *Fucus* by comparing results between study sites within countries as well as between Finland and Sweden.

Hypothesis 1 (H1): *Species community*.

Species community will be different in habitats dominated by algal mats of free-living *Fucus* compared to the surrounding bare soft bottom benthic habitats due to the habitat modifying effect of *F. vesiculosus*.

Hypothesis 2 (H2): *Abundance.*

Abundance of animals will be higher in habitats dominated by algal mats of free-living *Fucus* compared to the surrounding bare soft bottom benthic habitats.

Hypothesis 3 (H3): *Regional variation*.

There will be no regional difference in the effect of the presence of *Fucus* on the associated macrofauna between the two study regions.

Hypothesis 4 (H4): *Fucus size influence.*

The morphology of free-living *Fucus* will be influential in determining the community structure and functional groups present.

2. Materials and methods

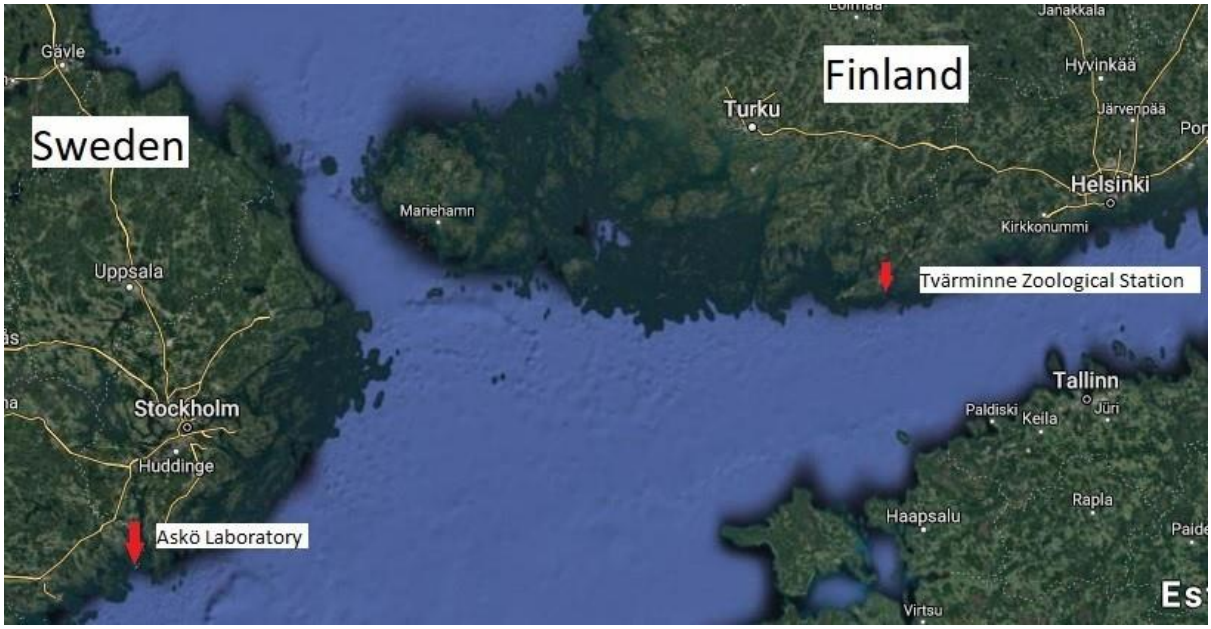
2.1. Research locations

For our study, we sampled from sites with present free-living *Fucus* from locations in two countries along the coast of the Baltic Sea: (1) Tvärminne Zoological Station (hereafter TZS) in southwestern Finland, and (2) Askö Laboratory (hereafter Askö) in eastern Sweden (Figure 3). The two stations are 330 km apart, Askö being 100 km south of TZS (Figure 3, A). Sampling was performed at sites where the presence of free-living *Fucus* was known, and coordinates of each site were noted using a GPS (Figure 3, B+C). To test the consistency of our results, both within and between the countries, we chose to sample at three different sites in each country. All sites were shallow and sheltered embayments within close proximity of the shore. The adjacent shore of all sites had a presence of *Phragmites australis* (Cav.) reeds, and *Fucus* thalli at sites A1 and T1 were tangled within the reeds (Figure 3, D).

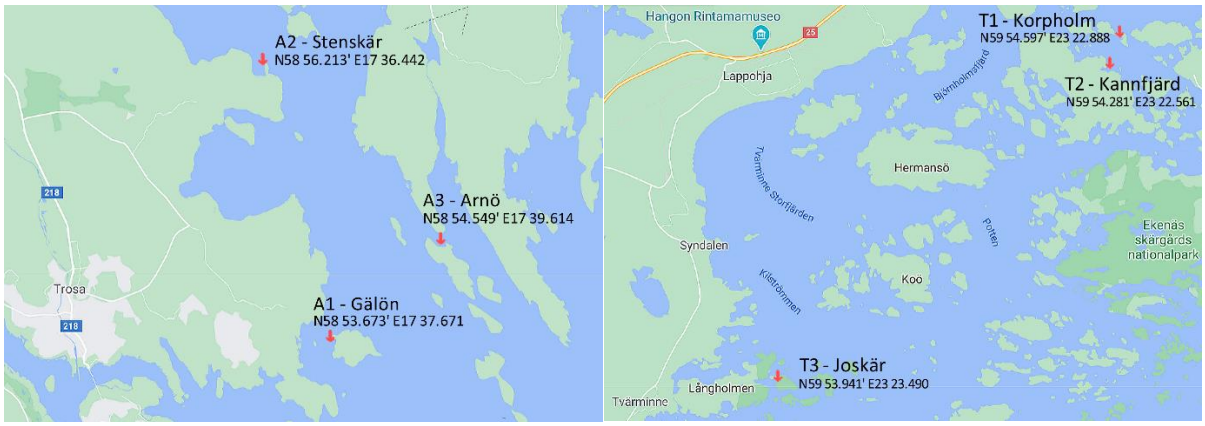
2.2. Sample collection

Samples were collected in June 2019 (TZS: 1-2.6.2019; Askö: 13.6.2019) by SCUBA diving at depths ranging from 1.5-4 m. Within each site, three random *Fucus* replicates were collected using frames with attached mesh bags. Each frame measured 30x30 cm with accompanying mesh bags having a mesh size of <1 mm. Within the frame, all vegetation and the associated epifaunal community were collected.

Macroinfaunal samples were randomly collected using circular benthic cores of 5.6 cm diameter, 10 cm deep. Three replicates were collected from two habitats: (1) under the *Fucus* mat (hereafter "*Fucus* infauna") and (2) bare sediment within 10 m of *Fucus* mat (hereafter "Control infauna") for a total of six infaunal replicates per site.



A



B C

D

Figure 3. A. Map of sampling zones. B. Askö site locations with coordinates. C. TZS site locations with coordinates. D. Photograph of Phragmites australis at the shore of site A3 in Sweden. Image source A-C: Google maps. Photo D by Roxana Preston.

2.3. Sample sorting

2.3.1. Epifauna

Fucus thalli were cleaned by rinsing with filtered marine water on top of a 0.8 mm sieve to remove all loose epiphytes and epifauna. Frames were sieved fresh during the following days from sampling. Unprocessed frames were kept in the shade before sieving.

During cleaning all visible fauna (hereafter "*Fucus* epifauna" were picked out and the remaining unsieved sampling material was checked under a light microscope (Nikon SMZ 745, 10x magnification). Collected animals were preserved in 70 % ethanol. Animals were counted and identified under a light microscope.

2.3.2. Infauna

Infaunal samples were rinsed with filtered marine water using a 0.5 mm sieve to remove all visible fauna and the remaining unsieved sampling material was checked under a light microscope (Nikon SMZ 745, 10x magnification). Animals were preserved in 70 % ethanol. Samples were sieved fresh during following days after sampling and were kept in shade before processing.

2.3.3. Morphological measurements

Cleaned *Fucus* frames from TZS were stored with a wet paper wipe in plastic bags at a maximum of 10 ^{o}C. Morphological measurements were taken within a week from sampling. Cleaned *Fucus* frames from Askö were stored in plastic bags in a freezer and were defrosted before morphological measurements were taken.

For morphological measurements, the whole frame was blot wet weighed (Mettler Toledo PB1501-S/FACT, accuracy of 1 g). Next, up to five *Fucus* thalli were separated from each frame (n = 120). The thallus length was measured from each thallus and the average thallus length was calculated for each frame. Thallus height (cm) was measured from the base of the holdfast to the tip of the most distal apex (modified measurements from Ruuskanen & Bäck 1999).

2.3.4. Animal identification

Animals were identified and counted using a light microscope (Nikon SMZ 745, 10x magnification) to the lowest possible taxa. Animals without shell (polychaetes, crustaceans, and others) were blot wet weighed (Mettler Toledo PG403-S, accuracy of 0.001 g). Molluscs and gastropods were measured using millimetre paper (accuracy of 1 mm) at their length of growth (anterior-posterior length). Up to 100 individuals of each species were measured per sample, the rest were counted, and the weight of all individuals was standardized according to the weight of the counted 100.

Biometric conversion factors for invertebrates of the Baltic Sea (Rumohr et al 1987) were used to convert biomass for most invertebrate species (dry weight, DW g/m^2). Some species had no conversion factors (e.g. *Palaemon elegans*, *Marenzelleria spp*, *Lymnea stagnalis*) and their presence is reported as densities (individuals m^{-2}).

2.4. Data analysis

All measured variables (animal abundance, biomass, *Fucus* wet weight) were first converted to m^2 for the analyses. Following analyses were performed using the vegan package in R version 4.0.3 (R Core Team 2020).

The Multiple Response Permutation Procedure (MRPP) ordination was used to analyse if there was a significant difference in the macrofaunal assemblages across countries and sites. These analyses were done individually for all three macrofaunal assemblages (*Fucus* epifauna, *Fucus* infauna, Control infauna) by comparing the assemblages of Askö and TZS. The contribution of individual taxa to the dissimilarities of the faunal community between sites and infauna habitat types were identified using the similarity percentages analysis SIMPER.

Two-way analyses of variance (ANOVA) were used to determine what factors influenced the number of taxa present, animal abundance and animal biomass. Used factors were Country (fixed, 2 levels, Askö vs TZS), Habitat (only for infauna, fixed, 2 levels, *Fucus* infauna vs Control infauna) and site (nested in country). If ANOVA showed significant differences ($p < 0.05$), a *post hoc* Tukey HSD test was performed.

Linear regression analyses were used to assess the effect of *Fucus* height and wet weight on the epifaunal abundance and biomass.

3. Results

3.1. *Fucus* morphology

Free-living *Fucus* was smaller in Askö (Sweden) than in TZS (Finland). The average height of *Fucus* thalli in Askö was 18.5 cm, whereas the average height in TZS was almost 5 cm taller, 23.3 cm. The average wet weight of *Fucus* in Askö was 1147.3 g m^{-2}, and the average weight in TZS was 1415.8 g m^{-2} (Table 1). ANOVA results, however, did not highlight significant differences between the *Fucus* morphology of the two countries. Only Site (Country) had a significant effect on *Fucus* height (Table 2).

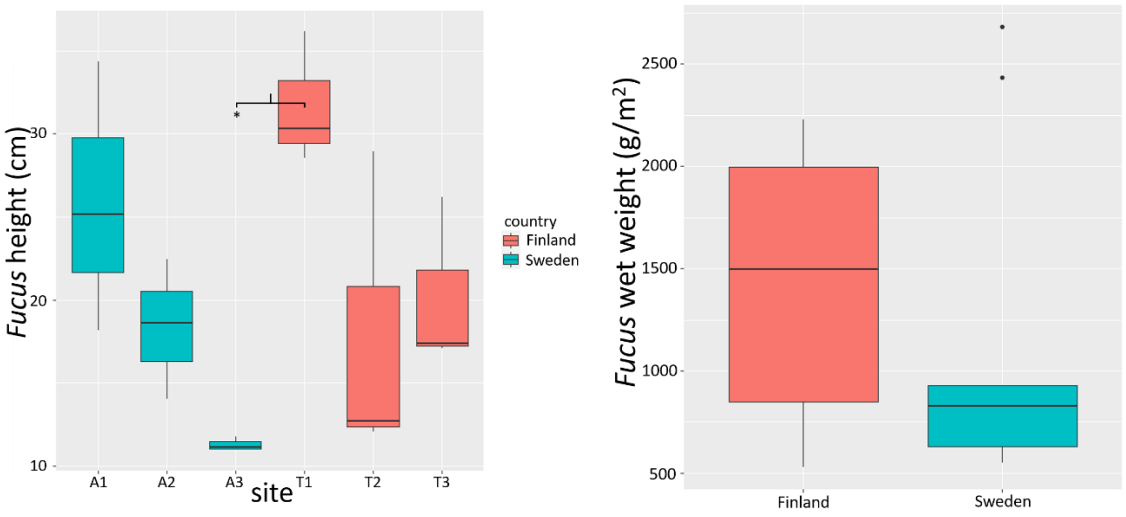
Table 1. The average, median and standard deviation (SD) of the weight and height of *Fucus* thalli in Askö (Sweden) and TZS (Finland).

	Height (cm)		**Wet weight (g m^{-2})**	
	Askö	*TZS*	*Askö*	*TZS*
average	18.5	23.3	1147.3	1415.8
median	18.2	26.2	829.1	1497.3
SD	7.4	8.1	767.8	622.3

Table 2. Summary of ANOVA results for *Fucus* height and wet weight, with Country (fixed factor) and Site (nested in Country). Significant results ($p < 0.05$) are in bold.

Source		***Fucus* height**			***Fucus* wet weight**		
	df	MS	F value	P value	MS	F value	P value
Country	1	101.41	2.792	0.1206	324549	0.555	0.470
Site (Country)	4	161.56	4.448	**0.0196**	444460	0.760	0.571
Residuals	12	36.32			584439		

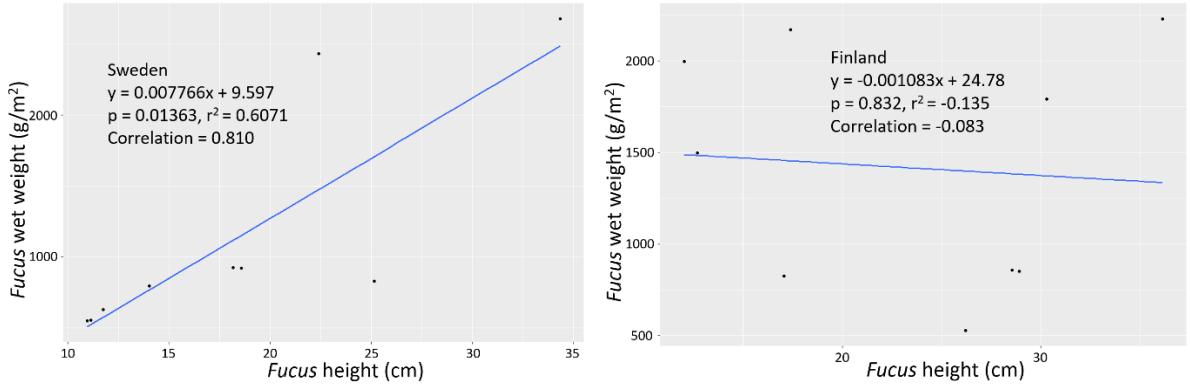
Tukey HSD post hoc comparisons of significant ANOVA results highlighted a significant difference in *Fucus* height between sites A3 and T1 (Figure 4, A). *Fucus* wet weight had no significant differences between sites or countries (Figure 4, B).



A B

Figure 4. Mean (± standard error, n=3) *Fucus* height per site (cm) (A) and mean (± standard error, n=9) *Fucus* wet weight by country (g m^{-2}) (B). Blue = Sweden, red = Finland. Horizontal lines connect statistically different sites and asterisks indicate the degree of significance determined by two-way ANOVA tests and Tukey HSD post hoc tests (*p < 0.05, **p < 0.01, ***p < 0.001).

The free-living population of *Fucus* in Askö had a significant relationship between height and wet weight (p = 0.014) (Figure 5, A). The population of TZS had no such relationship (Figure 5, B).



A B

Figure 5. Regressions showing the relationship between height (cm) and wet weight (g m^{-2}) of *Fucus*. A: Askö, B: TZS.

3.2. Multivariate analyses

The Multiple Response Permutation Procedure (MRPP) analysis tests if there is a significant difference between two groups. The analysis provides two values: the A-value and the p-value (delta). If A>0, the within-group similarity is greater than expected. We tested the similarity of sites (three samples per site) and countries (three sites per country; Sweden: Askö, Finland: TZS) for each macrofaunal assemblage (*Fucus* epifauna, *Fucus* infauna, Control infauna).

3.2.1. Epifaunal assemblages

The analyses of taxal abundance of the macroepifaunal assemblages (taxa-specific abundance) associated to free-living *Fucus* (*Fucus* epifauna) indicated a clear distinction between sites and

countries. Sites grouped within themselves (A=0.2259, p=0.004) and countries formed their own individual groups (country: A=0.1493, p=0.001) (Figure 6).

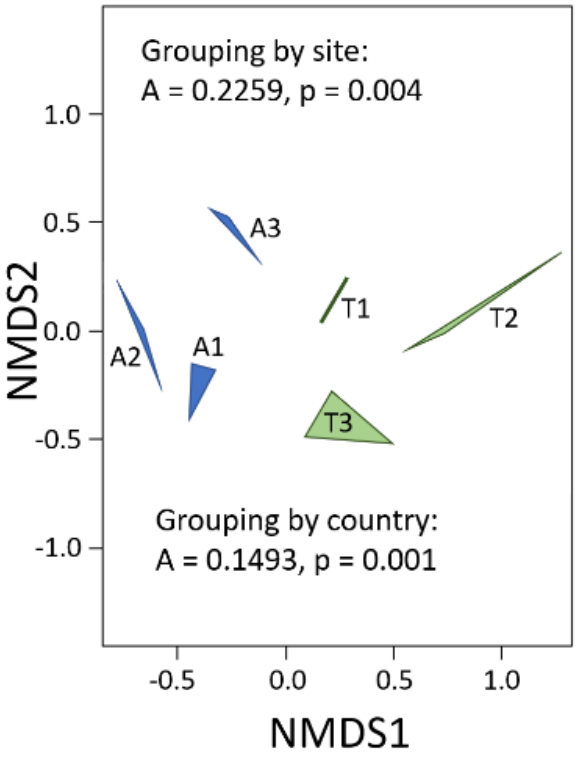


Figure 6. MRPP ordination of taxa-specific abundance of the epifaunal community of free-living *Fucus* (epifauna). Three samples per site are shown. Coordinates are shown as NMDS (Non-Metric Multidimesional Scaling) ordination, based on the dissimilarity matrix between sites. Blue = Askö (A), green = TZS (T).

The species contributing the most to differences between sites in Askö was *Peringia* spp. In TZS, *Balanus improvisus* (Darwin) contributed the most to differences between sites (SIMPER, Table 3).

Table 3. SIMPER results indicating the proportional contribution (%) of epifaunal taxa to the differences of the faunal composition between sites of a country (Sweden: Askö; Finland: TZS). The highest contributing taxa are in bold.

Taxa	Askö			TZS		
	A1:A2	A1:A3	A2:A3	T1:T2	T1:T3	T2:T3
Balanus improvisus				**35.9**	**42.4**	**36.6**
Chironomidae spp		11.7				
Peringia spp	**24.8**	**21.8**	**26.5**	25.3	16.7	13.6
Juvenile gastropod	9.8	10.3	22.8			
Limecola balthica			6.1			
Mytilus edulis	22.8	21.2				
Oligochaeta spp	15.5	13.2	10.5			
Parvicardium hauniense			9.2			
Theodoxus fluviatilis				18.5	18.8	28.3

3.2.2. Infaunal assemblages

The MRPP analyses of the macroinfaunal assemblages (taxa-specific abundance) associated to free-living *Fucus* (*Fucus* infauna) showed Askö sites grouping together, whereas TZS sites were

comparatively more scattered as site T3 grouped closer to Askö sites. Sites were not grouping independently (A=0.06534, p=0.122) due to overlap and relative scattering of sites A2 and T1. Countries were marginally significantly grouped within themselves (A=0.03518, p=0.08) (Figure 7).

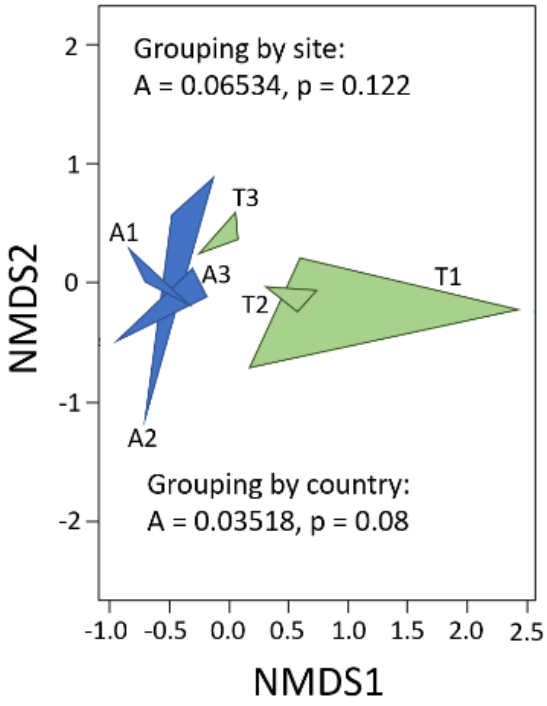


Figure 7. MRPP ordination of taxa-specific abundance of the macroinfaunal community of free-living *Fucus* (*Fucus* infauna). Three samples per site are shown. Coordinates are shown as NMDS (Non-Metric Multidimesional Scaling) ordination, based on the dissimilarity matrix between sites. Blue = Askö (A), green = TZS (T).

The MRPP analyses of the macroinfaunal assemblages (taxa-specific abundance) of the bare sediment (Control infauna) indicated that sites group significantly within themselves (A=0.5321, p=0.001). The two countries grouped together significantly within themselves (A=0.08694, p=0.017) (Figure 8).

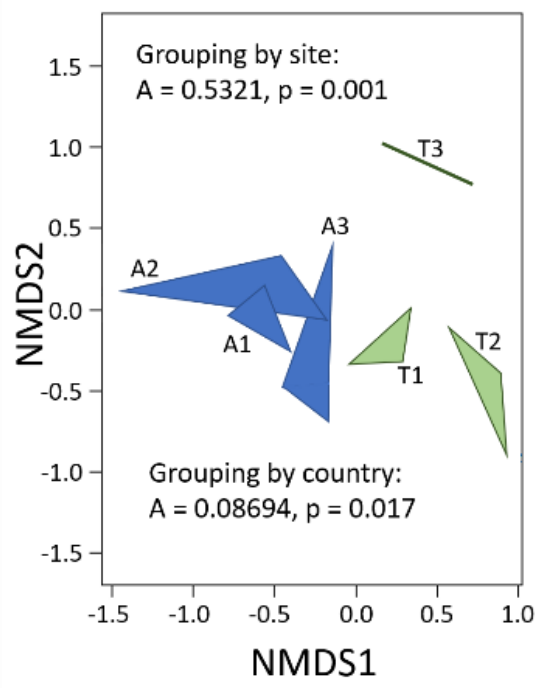


Figure 8. MRPP ordination of taxa-specific abundance of the macroinfaunal community of bare sediment (Control infauna). Three samples per site are shown. Coordinates are shown as NMDS (Non-Metric Multidimesional Scaling) ordination, based on the dissimilarity matrix between sites. Blue = Askö (A), green = TZS (T).

In Askö, a total of three taxa contributed to the differences of faunal composition between sites in *Fucus* infauna, with *Oligochaeta* spp. contributing the most (Table 4). A total of four taxa contributed to the differences of faunal composition between sites in Control infauna, with *Peringia* spp. contributing the most (Table 4). Three taxa contributed to the difference between assemblages of *Fucus* and Control infauna in Askö, with *Peringia* spp. contributing the most (Table 4).

Table 4. SIMPER results indicating the proportional contribution (%) of macroinfaunal taxa to the differences of faunal composition between sites and habitats (*Fucus* infauna and Control infauna) of Askö (Sweden). The most contributing taxa are in bold.

Askö	*Fucus*			Control			
	A1:A2	A1:A3	A2:A3	A1:A2	A1:A3	A2:A3	Sample:Control
Peringia spp	18.6	28.3	18.0	**56.1**	**62.9**	**29.6**	**40.1**
Hediste diversicolor	10.6					8.2	
Oligochaeta spp	**45.2**	**43.6**	**54.4**	18.3	14.1	21.4	26.2
Ostracoda spp						16.5	9.2

In TZS, a total of nine taxa contributed to the differences of faunal composition between sites in *Fucus* infauna, with *Peringia* spp and *Limecola balthica* (Linnaeus) contributing the most (Table 5). A total of four taxa contributed to the differences of faunal composition between sites in Control infauna, with *L. balthica* and *Oligochaeta* spp. contributing the most (Table 5). Five taxa contributed to the difference between the assemblages of *Fucus* and Control infauna, with *Oligochaeta* spp. contributing the most (Table 5).

Table 5. SIMPER results indicating the proportional contribution (%) of macroinfaunal taxa to the differences of faunal composition between sites and habitats (*Fucus* infauna and Control infauna) of TZS (Finland). The most contributing taxa are in bold.

TZS	*Fucus*			Control			
	T1:T2	T1:T3	T2:T3	T1:T2	T1:T3	T2:T3	Sample:Control
Balanus improvisus			5.1				
Bithynia spp			5.1				
Chironomidae spp	6.6	6.2				18.5	6.1
Peringia spp	**33.0**	22.7	15.3				20.5
Limecola balthica		**26.6**	**28.4**	17.5	8.4	**43.5**	16.4
Marenzelleria sp						22.7	
Oligochaeta spp	12.7		12.0	**62.3**	**64.3**		**25.3**
Ostracoda spp	14.0	9.5	7.6				7.7
Theodoxus fluviatilis	8.7	7.3					

3.3. Community characteristics of epifauna

A total of 29 epifaunal taxa were found associated to patches of *Fucus* in Askö: 7 Crustacea, 4 Insecta, 11 Mollusca, 1 Nemertea, 1 Platyhelminthes, 3 Annelida, 2 Vertebrata. The number of taxa per site ranged from 17 (A2) to 21 (A1) (Table 6). The dry weight of 16 taxa were measured using conversion factors, ranging from 108 g m^{-2} (A2) to 183 g m^{-2} (A1) (Supp. Table S1). A total of 31 epifaunal taxa were found in TZS: 8 Crustacea, 6 Insecta, 11 Mollusca, 1 Nemertea, 3 Annelida, 2 Vertebrata. The number of taxa per site ranged from 17 (T2) to 23 (T1) (Table 6). The dry weight of 16 taxa were measured using conversion factors, ranging from 49 g m^{-2} (T3) to 106 g m^{-2} (T1) (Supp. Table S1).

Table 6. Mean and standard error (number of individuals m^{-2}, ± standard error) of the abundances of epifaunal taxa associated to free-living *Fucus* collected in Sweden (Askö, three sites A) and Finland (TZS, three sites T).

Epifauna	Askö						TZS					
Taxa	A1		A2		A3		T1		T2		T3	
	mean	*se*	*mean*	*se*	*mean*	*se*	*mean*	*se*	*mean*	*se*	*mean*	*se*
CRUSTACEA												
Gammarus spp.	74	35	48	27	141	52	115	21	181	95	263	134
Asellus aquaticus	0	0	0	0	0	0	56	56	4	4	0	0
Balanus improvisus	19	13	37	20	0	0	2800	1972	33	19	2711	1453
Ostracoda spp.	11	6	22	22	0	0	0	0	4	4	0	0
Palaemon elegans	0	0	0	0	0	0	0	0	0	0	4	4
Idotea balthica	0	0	0	0	0	0	0	0	0	0	4	4
Jaera albifrons	0	0	0	0	0	0	0	0	0	0	4	4
Insect larvae sp.	0	0	0	0	0	0	0	0	0	0	7	7
Tanaid sp.	33	11	0	0	52	36	0	0	0	0	0	0
Copepod sp.	4	4	0	0	0	0	0	0	0	0	0	0
Idotea chelipes	0	0	4	4	4	4	0	0	0	0	0	0
Idotea sp.	0	0	0	0	7	4	0	0	0	0	0	0
INSECTA												
Trichoptera spp.	48	16	4	4	22	22	52	26	70	32	67	11
Chironomidae spp.	848	298	207	90	22	13	122	106	7	7	215	88
Diptera sp pupa	37	10	52	4	7	4	11	11	0	0	19	13
Zygoptera spp.	0	0	7	7	7	4	26	4	96	44	78	45
Plecoptera sp.	0	0	0	0	0	0	0	0	7	7	0	0
Insecta sp.	0	0	0	0	0	0	0	0	0	0	4	4
MOLLUSCA												
Theodoxus fluviatilis	100	63	330	114	333	34	1367	341	1737	464	193	150
Potamopyrgus antipodarium	0	0	0	0	56	32	126	29	0	0	156	95
Peringia spp.	2619	1115	2841	760	2652	245	1722	643	226	107	941	60
Bithynia spp.	4	4	0	0	0	0	104	53	63	32	4	4
Radix spp.	15	4	0	0	0	0	4	4	30	24	56	22
Parvicardium hauniense	507	276	437	316	93	38	67	28	11	11	0	0
Mytilus edulis	1737	741	100	13	156	36	26	15	22	0	11	6
Limecola balthica	0	0	0	0	219	55	152	38	26	13	81	66
Juvenile gastropod spp.	622	310	756	381	33	17	33	23	0	0	196	54
Lymnaea stagnalis	4	4	0	0	0	0	4	4	7	4	0	0
Cerastoderma glaucum	0	0	0	0	0	0	19	19	0	0	11	6
Mya arenaria	0	0	0	0	30	10	0	0	0	0	0	0
NEMERTEA												
Cyanopthalma obscura	81	61	0	0	7	7	4	4	0	0	0	0
PLATYHELMINTHES												
Turbellaria sp.	0	0	11	11	0	0	0	0	0	0	0	0
ANNELIDA												
Marenzelleria sp.	7	4	4	4	30	13	22	6	0	0	0	0
Manayunkia aestuarina	0	0	0	0	0	0	4	4	0	0	0	0
Hediste diversicolor	4	4	0	0	11	6	0	0	0	0	0	0
Oligochaeta spp.	1456	1049	626	259	533	131	48	23	0	0	4	4
VERTEBRATA												
Neogobius melanostomus	0	0	0	0	0	0	4	4	0	0	0	0
Gasterosteus aculeatus	11	6	0	0	0	0	0	0	7	4	0	0
Fish larvae sp.	0	0	37	37	0	0	0	0	0	0	0	0
TOTAL TAXA	21		17		20		23		17		21	

Results of ANOVA analyses indicated that Site (Country) had a significant effect on the total number of taxa ($p = 0.015$), but no significant differences for animal abundance or biomass (Table 7).

Table 7. Summary of ANOVA results for number of taxa, animal abundance and animal biomass of the epifauna community. Country (fixed factor) and Site (nested in country). Significant results ($p < 0.05$) are in bold.

Source		**Total taxa**			**Abundance**			**Biomass**		
	df	MS	F value	P value	MS	F value	P value	MS	F value	P value
Country	1	0.22	0.048	0.830	56001	0.570	0.465	1757.5	3.118	0.103
Site (Country)	4	88.89	4.819	**0.015**	105396	1.073	0.412	394.8	0.701	0.606
Residuals	12	4.611			98196			563.6		

Tukey HSD post hoc comparisons of significant ANOVA results highlighted the difference of site A2 from other Askö sites (Figure 9, A). Animal abundance and biomass showed no significant differences between sites or countries (Figure 9, B+C).

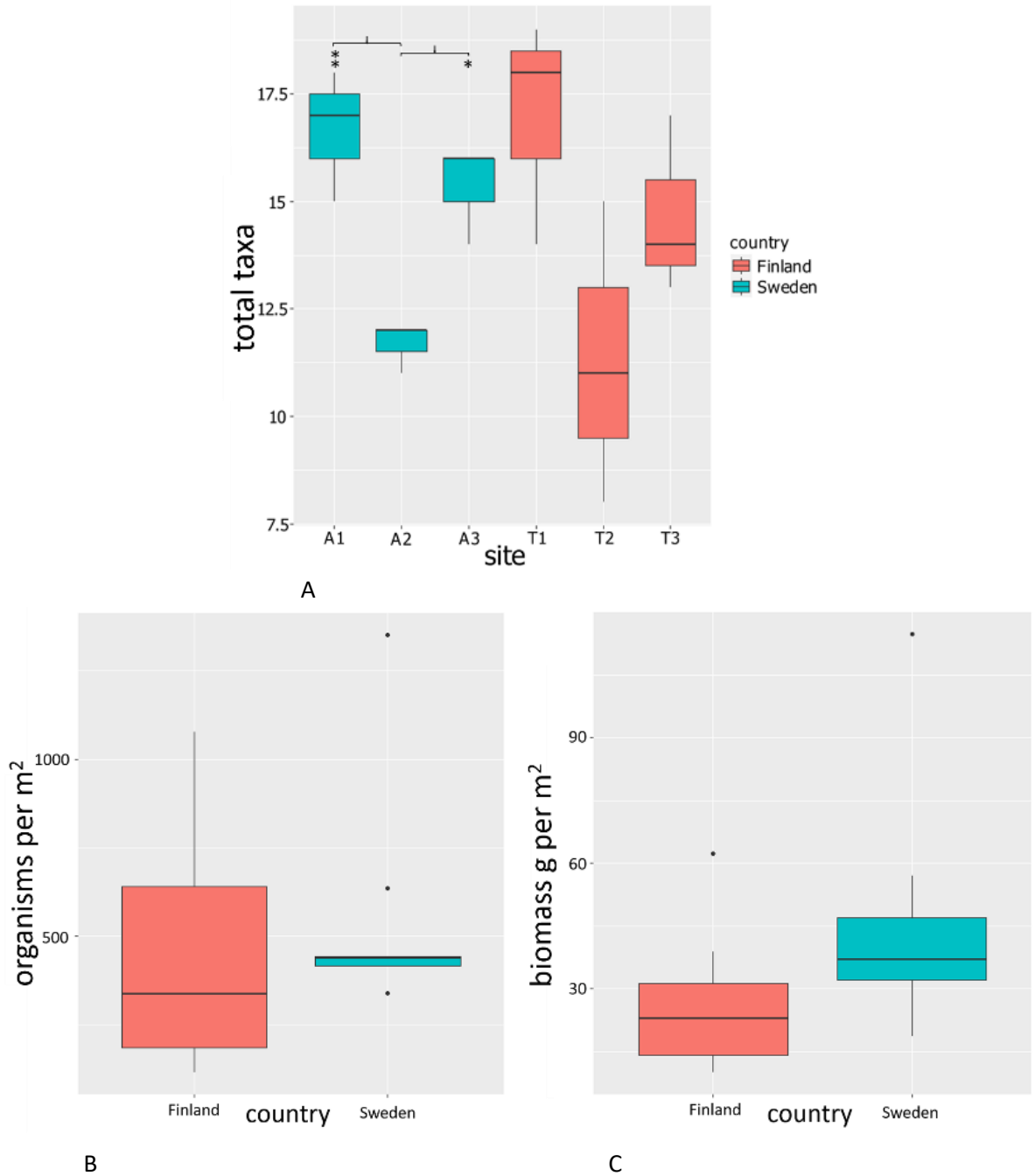


Figure 9. Mean (± standard error, n=3) total number of epifaunal taxa per site (A), mean (± standard error, n=9) epifaunal abundance by country (organisms m^{-2} (B) and mean (± standard error, n=9) epifaunal biomass by country (dry weight g m^{-2}) (C). Blue = Sweden, red = Finland. Horizontal lines connect statistically different sites and asterisks indicate the degree of significance determined by two-way ANOVA tests and Tukey HSD post hoc tests (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

3.4. Community characteristics of infauna

A total of 10 infaunal taxa were found associated to patches of *Fucus* in Askö: 1 Crustacea, 1 Insecta, 5 Mollusca, 3 Annelida. The number of taxa per site varied between six (A1 + A3) and seven (A2) (Table

8). The dry weight of six taxa were measured using conversion factors, ranging from 66 g m^{-2} (A3) to 249 g m^{-2} (A1) (Supp. Table S2). A total of 17 infaunal taxa were found associated to *Fucus* in TZS: 3 Crustacea, 2 Insecta, 6 Mollusca, 1 Nemertea, 4 Annelida. The number of taxa per site varied between 10 (T2 + T3) and 11 (T1) (Table 8). The dry weight of 10 taxa were measured using conversion factors, ranging from 79 g m^{-2} (T1) to 541 g m^{-2} (T3) (Supp. Table S2).

Table 8. Mean and standard error (number of organisms m^{-2}, ± standard error) of the abundances of infaunal taxa associated to free-living *Fucus* collected in Sweden (Askö, three sites A) and Finland (TZS, three sites T).

Fucus infauna	Askö						TZS					
Taxa	A1		A2		A3		T1		T2		T3	
	mean	*se*	*mean*	*se*	*mean*	*se*	*mean*	*se*	*mean*	*se*	*mean*	*se*
CRUSTACEA												
Gammarus spp.	0	0	0	0	0	0	0	0	541	271	0	0
Balanus improvisus	0	0	0	0	0	0	406	406	0	0	541	541
Ostracoda spp.	0	0	135	135	135	135	2030	2030	1083	1083	135	135
INSECTA												
Chironomidae spp.	0	0	0	0	135	135	947	488	406	0	135	135
Insect larvae sp.	0	0	0	0	0	0	0	0	271	271	0	0
MOLLUSCA												
Theodoxus fluviatilis	0	0	0	0	0	0	677	677	406	234	0	0
Potamopyrgus antipodarium	0	0	0	0	0	0	0	0	0	0	271	271
Peringia spp.	2030	620	812	469	1489	1108	1353	1353	4466	1074	3248	938
Bithynia spp.	0	0	0	0	0	0	135	135	541	358	0	0
Parvicardium hauniense	0	0	0	0	0	0	0	0	135	135	0	0
Mytilus edulis	135	135	0	0	0	0	0	0	0	0	0	0
Limecola balthica	271	271	541	271	812	406	541	358	271	135	3654	845
Juvenile gastropod spp.	271	271	0	0	0	0	0	0	0	0	0	0
Mya arenaria	0	0	135	135	0	0	0	0	0	0	0	0
NEMERTEA												
Cyanopthalma obscura	0	0	0	0	0	0	135	135	0	0	541	541
ANNELIDA												
Oligochaeta spp.	2030	1641	3383	3383	3113	947	947	488	2165	823	677	271
Marenzelleria sp	0	0	406	234	0	0	0	0	0	0	406	406
Manayunkia aestuarina	0	0	0	0	0	0	135	135	0	0	0	0
Hediste diversicolor	812	234	135	135	677	135	0	0	0	0	406	234
UNIDENTIFIED												
Various animal pieces	0	0	0	0	0	0	541	541	0	0	0	0
TOTAL TAXA	6		7		6		11		10		10	

A total of 14 infaunal taxa were found in the bare sediment adjacent to *Fucus* in Askö: 4 Crustacea, 1 Insecta, 6 Mollusca, 3 Annelida. The number of taxa per site varied between 9 (A3) and 11 (A1) (Table 9). The dry weight of nine taxa were measured using conversion factors, ranging from 141 g m^{-2} (A3) to 518 g m^{-2} (A1) (Supp. Table S3). A total of 11 infaunal taxa were found in the bare sediment in TZS: 1 Crustacea, 1 Insecta, 4 Mollusca, 1 Nemertea, 4 Annelida. The number of taxa per site ranged from four (T2 + T3) to 10 (T1) (Table 9). The dry weight of six taxa were measured using conversion factors, ranging from 119 g m^{-2} (T3) to 1190 g m^{-2} (T1) (Supp. Table S3).

Table 9. Mean and standard error (number of organisms m^{-2}, ± standard error) of the abundances of infaunal taxa of bare sediment collected in Sweden (Askö, three sites A) and Finland (TZS, three sites T).

Control infauna	Askö						TZS					
Taxa	A1		A2		A3		T1		T2		T3	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	Se
CRUSTACEA												
Balanus improvisus	0	0	406	406	0	0	0	0	0	0	0	0
Ostracoda spp.	1489	358	1759	271	271	271	3113	3113	0	0	135	135
Tanaid sp.	0	0	0	0	135	135	0	0	0	0	0	0
Copepoda sp.	135	135	0	0	0	0	0	0	0	0	0	0
INSECTA												
Chironomidae spp.	406	406	406	234	271	135	1218	406	947	358	0	0
MOLLUSCA												
Potamopyrgus antipodarium	0	0	0	0	0	0	541	541	0	0	0	0
Peringia spp.	16917	1374	4737	1759	2030	703	1353	488	0	0	0	0
Parvicardium hauniense	1218	620	271	135	0	0	0	0	0	0	0	0
Mytilus edulis	812	620	0	0	0	0	0	0	0	0	0	0
Limecola balthica	1083	358	677	358	541	271	4060	845	271	271	2436	234
Juvenile gastropod spp.	0	0	0	0	0	0	135	135	0	0	0	0
Cerastoderma glaucum	0	0	135	135	0	0	0	0	0	0	0	0
Mya arenaria	135	135	271	271	135	135	0	0	0	0	0	0
NEMERTEA												
Cyanopthalma obscura	0	0	0	0	0	0	541	358	0	0	0	0
ANNELIDA												
Oligochaeta spp.	4737	1374	541	541	2842	2044	18541	6565	541	358	0	0
Marenzelleria sp.	135	135	406	406	135	135	135	135	135	135	1218	620
Manayunkia aestuarina	0	0	0	0	0	0	135	135	0	0	0	0
Hediste diversicolor	677	271	0	0	812	0	0	0	0	0	0	0
Bylgides sarsi	0	0	0	0	0	0	0	0	0	0	135	135
TOTAL TAXA	11		10		9		10		4		4	

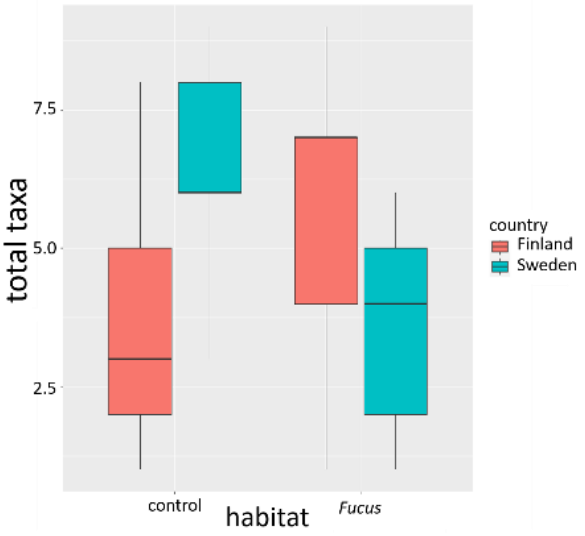
Results of two-way ANOVA analyses for macroinfauna indicate that the interaction of Habitat x Country has a significant effect on the number of taxa (Table 10). The Tukey HSD post hoc test however did not highlight any site or habitat as significantly different, and thus all sites of both habitats are pooled in Figure 10 (A).

The Habitat x Site (Country) interaction showed a significant effect on animal abundance (Table 10). In Askö, the abundance of macroinfauna at Control site A1 was significantly higher (Tukey HSD post hoc test) than the macroinfauna at the other Control sites (A2 and A3), and higher than the macroinfauna associated to *Fucus* of all sites (A1, A2 and A3) (Figure 10, B). In TZS, the abundance of macroinfauna at Control site T1 was significantly higher (Tukey HSD post hoc test) than the macroinfauna at the other Control sites (T2 and T3), and higher than the macroinfauna associated to *Fucus* of all sites (T1, T2 and T3) (Figure 10, B).

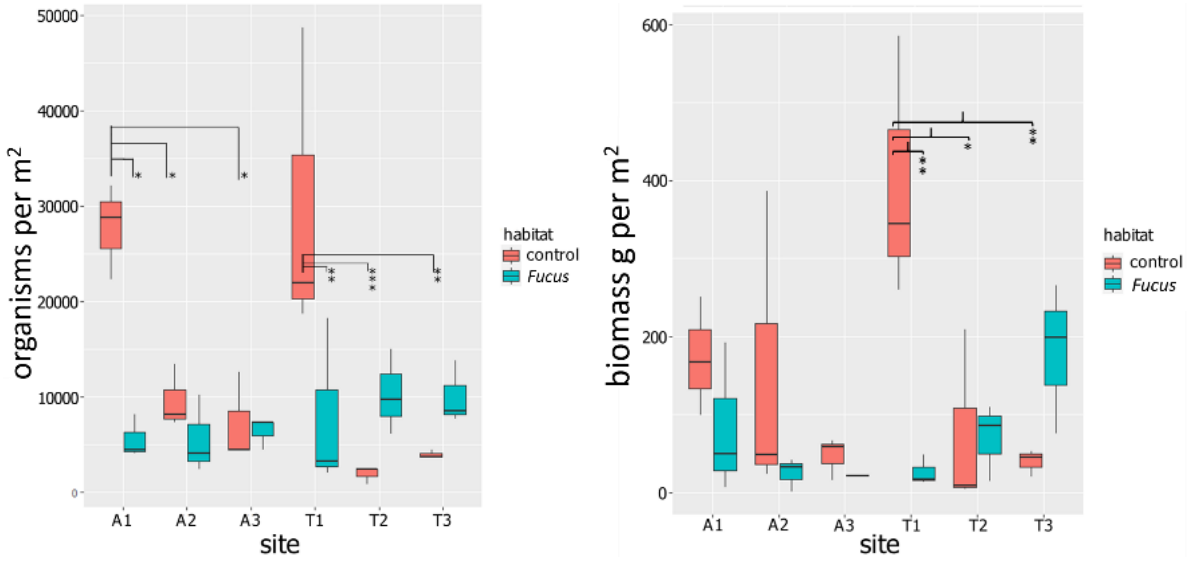
The abundance and biomass of macroinfauna showed a significant Habitat x Site (Country) (Table 10). In TZS, macroinfauna biomass of Control site T1 was significantly higher (Tukey HSD post hoc test) than the macroinfauna at the other Control sites (T2 and T3), and higher than the macroinfauna associated to *Fucus* of all sites (T1, T2 and T3) (Figure 10, C).

Table 10. Summary of ANOVA results for number of taxa, animal abundance and animal biomass of the infauna community. Habitat, Country (fixed factors) and Site (nested in Country). Significant results ($p < 0.05$) are in bold.

Source		Total taxa			Abundance			Biomass		
	df	MS	F value	P value	MS	F value	P value	MS	F value	P value
Habitat	1	1.36	0.345	0.562	297746025	7.640	**0.011**	56753	6.098	**0.021**
Country	1	1.36	0.345	0.562	773842	0.020	0.889	20194	2.170	0.154
Site (Country)	4	3.19	0.810	0.531	241663083	6.201	**0.001**	22233	2.389	0.079
Habitat x Country	1	51.36	13.021	**0.001**	96272360	2.470	0.129	19	0.002	0.965
Habitat x Site (Country)	4	9.19	2.331	0.085	313222866	8.037	**<0.001**	53997	5.801	**0.002**
Residuals	24		3.94		38971417			9308		



A



B C

Figure 10. Mean (± standard error, n=9) total number of taxa by country (A), mean (± standard error, n=3) animal abundance by site per habitat (Control infauna or *Fucus* infauna) (organisms m^{-2}) (B) and mean (± standard error, n=3) animal biomass by site per habitat (dry weight g m^{-2}) (C). Horizontal lines connect statistically different sites and asterisks indicate the degree of significance determined by two-way ANOVA tests and Tukey HSD post hoc tests (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

3.5. Effect of *Fucus* morphology on epifauna

Both height and wet weight of the free-living *Fucus* showed a significant and positive effect on animal abundance in Askö (Sweden) (Figure 11, A+B). The height of *Fucus* did not significantly affect the animal abundance in TZS (Finland) (Figure 11, C). The wet weight of *Fucus* had a significant and positive effect on the animal abundance in TZS (Figure 11, D).

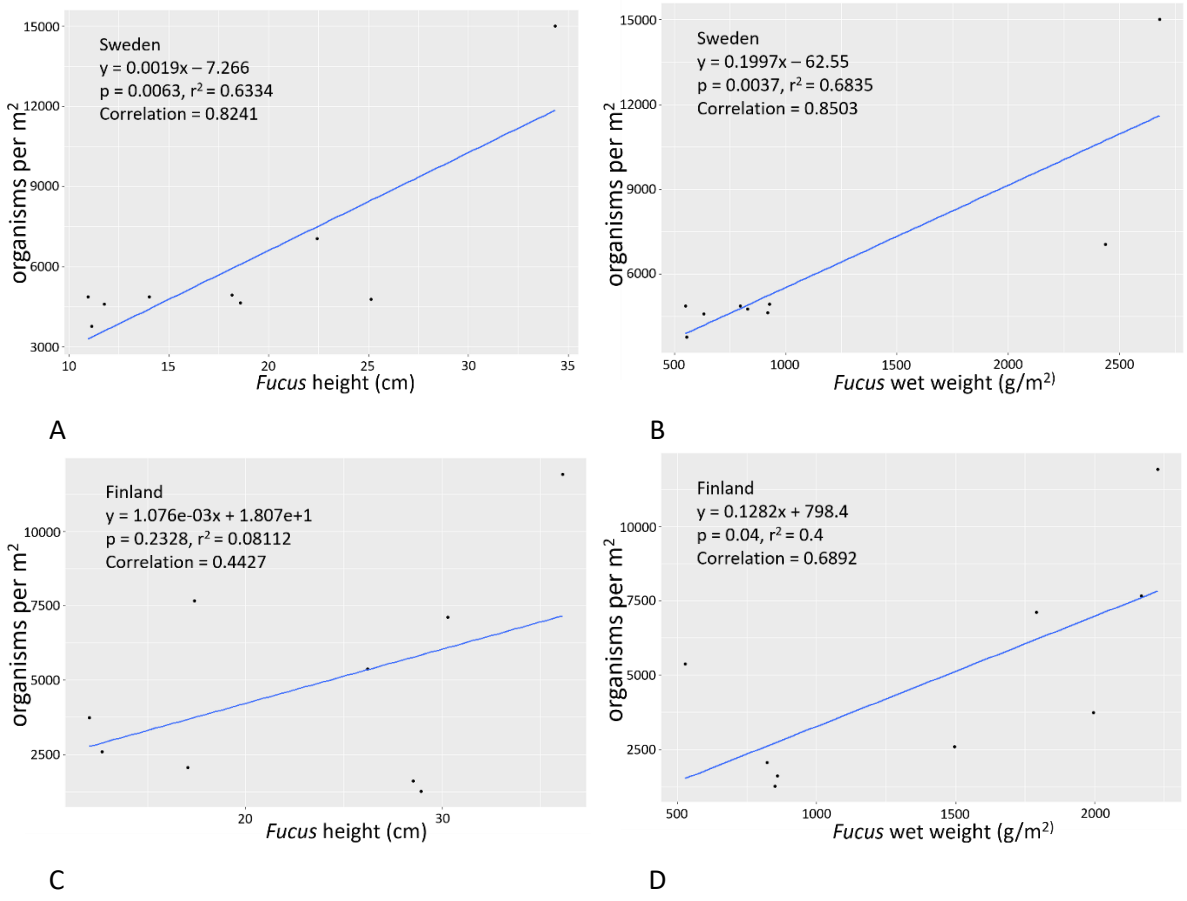


Figure 11. Regressions showing the relationship of animal abundance (organisms m^{-2}) with the height (cm) and wet weight (g m^{-2}) of free-living *Fucus*. A: Sweden (Askö) animal abundance and *Fucus* height. B: Sweden animal abundance and *Fucus* wet weight. C: Finland (TZS) animal abundance and *Fucus* height. D: Finland animal abundance and *Fucus* wet weight.

The height and wet weight of free-living *Fucus* showed a significantly positive effect on animal biomass in Askö (Figure 12, A+B). Neither the height nor the wet weight showed a significant effect on animal biomass in TZS, however *Fucus* wet weight showed a marginally significant (i.e. $0.10 < p < 0.05$) positive effect (Figure 12, C+D).

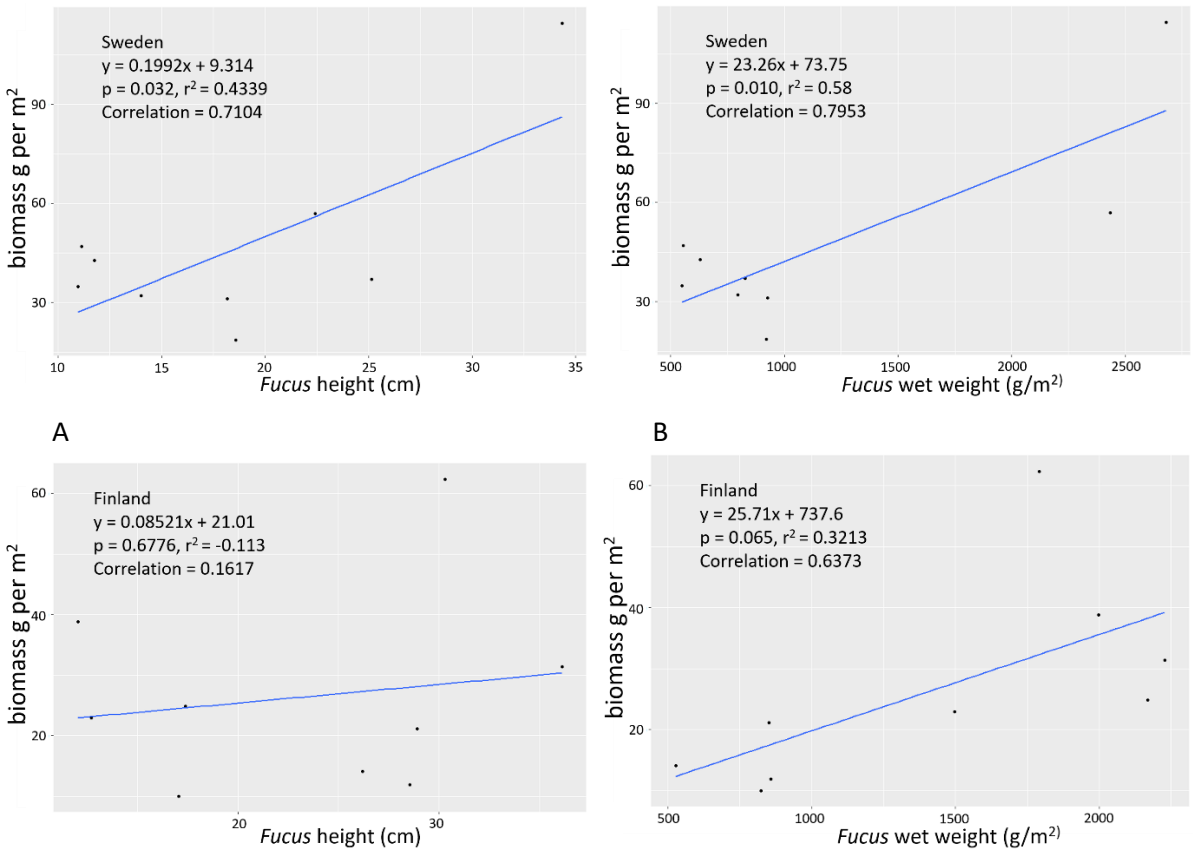


Figure 12. Regressions showing the relationship of animal biomass (g m^{-2}) with the height (cm) and wet weight (g m^{-2}) of free-living *Fucus*. A: Sweden (Askö) animal biomass and *Fucus* height. B: Sweden animal biomass and *Fucus* wet weight. C: Finland (TZS) animal biomass and *Fucus* height. D: Finland animal biomass and *Fucus* wet weight.

4. Discussion

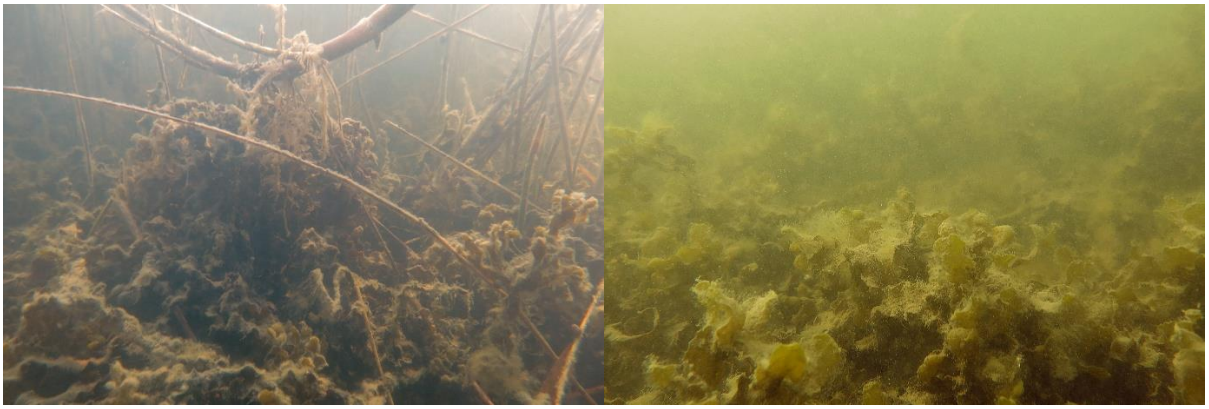
As little is known on the ecological role of free-living *Fucus vesiculosus* (*Fucus*), the main goal of this thesis was to investigate its associated macrofaunal community and thus reach a better understanding of its importance in sheltered, soft bottom habitats. Additionally, this study was the first comprehensive investigation of the macroepifaunal and macroinfaunal communities associated to free-living *Fucus.*

We studied the ecological role of free-living *Fucus* on its associated macroepifaunal and macroinfaunal communities by comparing them with the macroinfaunal community of adjacent bare sediment. For a more complete understanding of the spatial scale of the functional role of free-living *Fucus*, we collected samples at three different sites in two countries (Sweden and Finland). Understanding the influence of present *Fucus* on a spatial scale allows us to estimate its effect in a broader scope, rather than being only limited to a local understanding.

4.1. The effect of *Fucus* on infauna

Multivariate analyses based on the dissimilarity of the macrofaunal assemblages indicated that the macroinfaunal community associated to free-living *Fucus* did not vary significantly on a geographical scale (Figure 7). Due to the low number of present taxa in the macroinfaunal assemblages, the presence or absence of only a few taxa stands out. The *Fucus* infauna at site T3 resembles Askö sites due to the absence of gastropod *Theodoxus fluviatilis* and presence of polychaete *Hediste diversicolor*, possibly indicating abiotic conditions not accounted for in our study. Geographical distance significantly affects the macroinfaunal assemblage of bare sediment, as both sites and countries share significant similarity within themselves when compared to each other (Figure 8).

According to our results, the presence of *Fucus* did not significantly affect the number of present taxa of macroinfauna (Figure 10, A). The abundance of bare sediment infauna showed high variation within both countries, with Control infauna at both sites A1 and T1 showing significantly higher infauna abundance than adjacent *Fucus* infauna and other sites. This may be due to the presence of *Phragmites australis* reeds within the sampling area, as these sites were the only ones where *Fucus* was close enough to the shore to be entangled within the reeds, despite *P. australis* being present at the shore of every site. The Control infauna community at both sites was dominated by opportunistic taxa (*Peringia* spp. in Sweden, *Oligochaeta* spp. in Finland, Table 9).



A B

Figure 13. A. *Fucus* at site T1, showing algae tangled within *Phragmites australis* reeds. B. Untangled *Fucus* at site T2.

4.2. The effect of *Fucus* on epifauna

4.2.1. Community characteristics of epifauna

Multivariate analyses based on dissimilarity of macroepifaunal assemblages indicated that while the assemblage at each site is distinctive, the geographic distance between countries significantly affects the overall epifaunal community. The sites within both Sweden and Finland shared significant similarity when compared against each other. This finding is not surprising, as physical distance and several biotic and abiotic conditions are known to limit the dispersal of fauna and the macrofauna communities (Hubbell 2001).

Despite the natural dissimilarity of the epifaunal assemblage between the two countries, the overall effect of the presence of *Fucus* was consistent. The number of macrofaunal taxa did not vary between the two countries but varied significantly within Sweden and non-significantly within Finland (Figure 9, A), demonstrating some natural variation in the macroepifaunal community despite geographic distance. The diversity of macroepifaunal taxa varied between the two countries as well: a greater number of taxa contributed to the differences between sites in Sweden than in Finland (Table 3), implying that the Finnish epifaunal community is dominated by a few taxa, whereas the community of Sweden is more diverse.

Despite some variation in the taxa, animal abundance and biomass did not vary between sites nor countries (Figure 9, B+C). Our results demonstrate that free-living *Fucus* harbours a consistent number of macroepifaunal organisms and macroepifaunal biomass across our study area.

4.2.2. Effects of Fucus morphology on epifauna

According to our results, increasing *Fucus* height significantly increased both epifaunal abundance and biomass in Sweden, but not in Finland (Figure 11, A+C, Figure 12, A+C). Increasing *Fucus* wet weight significantly increased the epifauna abundance in both Sweden and Finland (Figure 11, B+D). Wet

weight also affected animal biomass in Sweden (Figure 12, B) and showed a marginally significant effect on epifaunal biomass in Finland (Figure 12, D).

Some differences between the epifaunal communities of the two countries may be due to morphological differences in the *Fucus* thalli. The structure of *Fucus* thalli may vary from dense and bushy to smoother and loose. Samples from Sweden showed a higher proportion of smaller, denser *Fucus* bushes (personal observations). This observation is supported by our data, which demonstrates a significant dependence of *Fucus* height and wet weight in Sweden but not in Finland (Figure 5, A+B). The average height and wet weight are smaller in Sweden than in Finland, although *Fucus* wet weight was not significant in analyses. *Fucus* height had significant differences between sites A3 and T1 (Figure 4, A).

4.2.3. Noteworthy taxa

A few taxa stood out as having remarkable variation between the two countries. *Balanus improvisus* was abundant at sites T1 and T3 in Finland, with only a few individuals found in Sweden (Table 6). This may be due to morphological differences between *Fucus* plants or abiotic factors, such as water flow or salinity which may affect the ability of *B. improvisus* to settle on a substrate (Berntsson et al 2000). However, we are unable to confirm whether *B. improvisus* colonization occurred before or after the settlement of *Fucus* in the study sites.

The gastropod *Theodoxus fluviatilis* (L.) was especially abundant in the epifauna at sites T1 and T2 despite being present across all study sites (Table 6). *Theodoxus fluviatilis* is a grazer that may be beneficial for the growth of *Fucus* by grazing on epiphytes (Råberg & Kautsky 2008). The sites where *T. fluviatilis* was abundant are geographically close (Figure 3, C).

We highlight the low abundance of isopods and the absence of *Idotea balthica* (Pallas) in the epifaunal community of free-living *Fucus,* with only one individual found at site T3. *Idotea balthica* is a significant grazer of the attached *Fucus* morph (Leidenberger et al 2012). However, Leidenberger et al (2012) reviewed the distribution patterns of *I. balthica* and found that its abundance is at a yearly low around May-June, with peak abundances around August. Tiblom (2017) found low abundances of *I. balthica* within patches of free-living *Fucus* even in August, suggesting that *I. balthica* may avoid free-living *Fucus*. However, low abundances of isopods may be due to other factors, such as water salinity or sampling procedure. Our study sites are close to freshwater outlets which may deter animals which prefer higher water salinity, and our sampling procedure may not be able to capture enough fast mobile animals to make strong conclusions. Assessing whether *I. balthica* avoids free-living *Fucus* and potential consequences will require further research. If *I. balthica* were to avoid the free-living morph,

it is essential to understand why to improve our understanding of the dynamic between these two fundamental species of the Baltic Sea.

Epifaunal samples A1 and A3 and bare sediment infauna from A3 in Sweden showed unidentified tanaids, which are likely one of two potential species (Figure 14). Two tanaid species are encountered in the Baltic Sea, the first being *Heterotanais oerstedi* which is the only tanaid native to the Baltic Sea. The documented distribution of *H. oerstedi* includes Swedish and Polish coasts in the southern and western Baltic Sea, with sightings up to southern Finland (Szaniawska 2018, WoRMS 2021). The second tanaid species is the invasive *Sinelobus vanhaareni*, which was first recorded in the Gulf of Gdansk in 2014, and since 2016 it has been found in Finland (Brzana et al 2019; personal observations). The species found in our samples is most likely *H. oerstedi*, as our Swedish sites fall within its natural range. However, it is possible that the species was in fact *S. vanhaareni*. In that case its habitat preference would need to be re-investigated, as Brzana et al (2019) established that *S. vanhaareni* prefers hard surfaces.

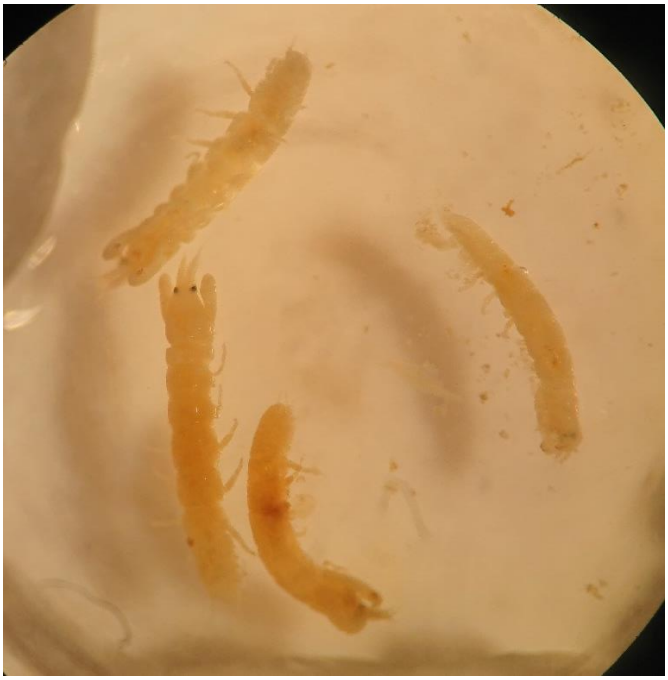


Figure 14. Unidentified tanaids from Sweden.

Our results showed that several important epifaunal taxa beneficial to fisheries were represented in the epifauna community of free-living *Fucus*. Several taxa present at all or almost all sites (*Chironomidae* spp, *Gammarus* spp, *Oligochaeta* spp) (Table 6) are important food items for several commercial fish species (Florin & Lavados 2010, Jakubavičiūtė et al 2017). Additionally, several *Fucus* samples showed fish eggs (personal observations) and site A2 showed representatives of fish larvae. Adult three-spined sticklebacks (*Gasterosteus aculeatus*) were present at several sites. Three-spined sticklebacks are an important food item for predatory fish such as pike and perch (Jacobson et al 2019),

and the presence of eggs and larvae confirm that free-living *Fucus* works as a fish nursery. As such, our results confirm that free-living *Fucus* provides important ecosystem services by providing a habitat for several food items of commercial fish.

4.3. Assessing hypotheses

The presence of free-living *Fucus* increased the diversity of the macrofaunal community by providing a potential habitat to the macroepifaunal community. Therefore, we can confirm Hypothesis 1 (taxal community will be different in habitats dominated by free-living *Fucus* compared to the surrounding bare soft bottom benthic habitats), as the taxal community in habitats dominated by *Fucus* have a higher diversity than the adjacent bare soft bottoms. However, the taxa of the macroinfaunal communities did not differ significantly and the observed variation of animal abundance and biomass are likely due to non-measured abiotic variables. It can therefore be concluded that free-living *Fucus* does not cause anoxic conditions in the sediment and is not detrimental to the macroinfaunal community.

Our results suggest that biotic and abiotic conditions other than the presence or absence of *Fucus* affects the macroinfaunal community. One possibility is the presence of reeds, which were present at sites with high abundances of Control infauna. As the highest animal abundance and biomass was recorded in the macroinfaunal assemblage of bare sediment, Hypothesis 2 (animal abundance will be higher in habitats dominated by *Fucus* compared to the surrounding bare soft bottom benthic habitats) must be rejected.

The presence of *Fucus* had the same effect in both countries. However, the magnitude of the effects caused by varying *Fucus* morphology was different in Sweden and in Finland, as both *Fucus* height and wet weight significantly increased animal abundance and biomass in Sweden, but only *Fucus* wet weight had an effect in Finland. As morphological characteristics elicited a clear response in both countries, we confirm Hypothesis 3 (the effect of *Fucus* on fauna will not vary between regions).

Our results show that the wet weight of both attached and free-living *Fucus* create a similar response on the abundance and biomass of epifauna (Korpinen et al 2010). Additionally, *Fucus* height may influence animal abundance and biomass. In the light of our results, Hypothesis 4 (Morphological differences in *Fucus* will have a significant effect on the epifaunal community structure) is confirmed.

5. Conclusions

As this study was the first time both the macroepifaunal and macroinfaunal communities of free-living *Fucus* has been investigated, our results provide a better understanding of the ecological role of free-

living *Fucus*. Hence, future environmental assessments of free living *Fucus* forms should take its functional role on the soft sediment macrofauna communities into account.

5.1. Governmental assessments

Previous governmental assessments regarding free-living *Fucus* have been made based on little knowledge about what (HELCOM 2013). This study provides new insights into the ecological role of free-living *Fucus* on the macroinfaunal community, particularly about the potential induced anoxia of the sediment (HELCOM 2013). Our data suggests that free-living *Fucus* does not cause anoxia in the sediment layer.

5.2. Importance of free-living *Fucus* and its protection

Our study demonstrates the free-living *Fucus* as a potential foundation species in the sheltered, shallow bays of the Baltic Sea. Its presence greatly increases the local taxa diversity compared to adjacent bare sediment, with increasing *Fucus* biomass directly increasing the animal abundance and biomass. Additionally, free-living *Fucus* was not found to have noticeable negative effects on the associated macroinfaunal community. This feature of increasing the local biodiversity in turn increases local ecosystem functioning, which translates to important ecosystem services (Balvanera et al 2006). Our study found that free-living *Fucus* harbours several fauna, of which many are preferred food items for both commercial and non-commercial fish, and works as both shelter and nursery for fish.

In the light of these findings, it is crucial to take these habitats into account in marine conservation planning. Protecting these habitats will require tackling the issue of anthropogenic activity and eutrophication. Mitigation of eutrophication will be critical when protecting both the attached and free-living morphs, especially since local extinctions have already happened in the Polish coast (HELCOM 2013, Takolander 2018, Barboza et al 2019, Kotta et al 2019).

5.3. Future research

As free-living *Fucus* is a potential foundation species in the sheltered soft bottom bays of the Baltic Sea, it is fundamental to gain a thorough understanding of its ecological role. Our work provides a first look into the associated faunal communities harboured by free-living *Fucus* and provides a starting point for future research. As of now, we lack understanding on the apparent lack of *I. balthica* in the epifaunal community of free-living *Fucus*. We also lack knowledge about the effect that different *Fucus* habitats (such as reeds) and *Fucus* patch sizes have on the faunal assemblages and oxygen conditions of the sediment.

Additionally, work is currently under way by thesis supervisor Roxana Preston on the origin and population structure of free-living *Fucus*. Some results have already been published on the genetic structure of some free-living populations (Aittamäki 2020).

To conclude, free-living *Fucus* is a fascinating but little understood organism that offers ample research opportunities for the future. Our study provides a basic understanding of the associated faunal community of free-living *F. vesiculosus* to be built upon.

6. Acknowledgements

I would like to express my deepest gratitude to my supervisors Dr. Iván Franco Rodil and MSc, Doctoral Student Roxana Preston for the invaluable support and advice throughout this Master's thesis. I am grateful to Walter and Nottbeck Foundation for providing me a study grant to fund this work. I also wish to thank David Israel for all the office hours and the Youtube channel Peaceful Ambience for their Pomodoro videos.

7. References

Aittamäki, A. (2020). Pohjoisen Itämeren vapaana elävien rakkohaurupopulaatioiden alkuperä ja lisääntyminen. Master's thesis. University of Helsinki. (in Finnish)

Attard, K. M., Rodil, I. F., Berg, P., Norkko, J., Norkko, A., & Glud, R. N. (2019). Seasonal metabolism and carbon export potential of a key coastal habitat: The perennial canopy-forming macroalga *Fucus vesiculosus*. *Limnology and Oceanography*, *64*(1), 149–164.

Austin, N., Hansen, J. P., Donadi, S., Bergström, U., Eriksson, B. K., Sundblad, G., & Eklöf, J. S. (2021). Synergistic Effects of Rooted Aquatic Vegetation and Drift Wrack on Ecosystem Multifunctionality. *Ecosystems*, 1–17.

Baden, S., Gullström, M., Lundén, B., Pihl, L., & Rosenberg, R. (2003). Vanishing Seagrass (*Zostera marina*, L.) in Swedish Coastal Waters. *AMBIO: A Journal of the Human Environment*, *32*(5), 374–377.

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D., & Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, *9*(10), 1146–1156.

Barboza, F. R., Kotta, J., Weinberger, F., Jormalainen, V., Kraufvelin, P., Molis, M., … Wahl, M. (2019). Geographic variation in fitness-related traits of the bladderwrack *Fucus vesiculosus* along the Baltic Sea-North Sea salinity gradient. *Ecology and Evolution*, *9*(16), 9225–9238.

Bauch, R. (1954). Biologisch-ökologische Stuclien an cler Gattung *Fucus*. *Flora Oder Allgemeine Botanische Zeitung*, *142*(1), 1–24. (in German)

Beck, M. W., Brumbaugh, R. D., Airoldi, L., Carranza, A., Coen, L. D., Crawford, C., … Guo, X. (2011). Oyster Reefs at Risk and Recommendations for Conservation, Restoration, and Management. *BioScience*, *61*(2), 107–116.

Belkin, I. M. (2009). Rapid warming of Large Marine Ecosystems. *Progress in Oceanography*, *81*(1–4), 207–213.

Berger, R., Henriksson, E., Kautsky, L., & Malm, T. (2003). Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. *Aquatic Ecology*, *37*(1), 1–11.

Bergström, L., Tatarenkov, A., Johannesson, K., Jönsson, R. B., & Kautsky, L. (2005). Genetic and morphological identification of *Fucus radicans* sp. nov. (Fucales, Phaeophyceae) in the brackish Baltic Sea. *Journal of Phycology*, *41*(5), 1025–1038.

Berntsson, K. M., Jonsson, P. R., Lejhall, M., & Gatenholm, P. (2000). Analysis of behavioural rejection of micro-textured surfaces and implications for recruitment by the barnacle *Balanus improvisus*. *Journal of Experimental Marine Biology and Ecology*, *251*(1), 59–83.

Bodkin, J. L. (1988). Effects of kelp forest removal on associated fish assemblages in central California. *Journal of Experimental Marine Biology and Ecology*, *117*(3), 227–238.

Bonsdorff, E., Blomqvist, E. M., Mattila, J., & Norkko, A. (1997). Coastal eutrophication: Causes, consequences and perspectives in the archipelago areas of the Northern Baltic Sea. *Estuarine, Coastal and Shelf Science*, *44*(SUPPL. A), 63–72.

Boström, C., Baden, S., Bockelmann, A., Dromph, K., Fredriksen, S., Gustafsson, C., … Rinde, E. (2014). Distribution, structure and function of Nordic eelgrass *(Zostera marina)* ecosystems: implications for coastal management and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*(3), 410–434.

Boström, C., & Bonsdorff, E. (1997). Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea. *Journal of Sea Research*, *37*(1–2), 153–166.

Brinkhuis, B. H., & Jones, R. F. (1976). The ecology of temperate salt-marsh fucoids. II. In situ growth of transplanted *Ascophyllum nodosum* ecads. *Marine Biology*, *34*(4), 339–348.

Brzana, R., Marszewska, L., Normant-Saremba, M., & Błażewicz, M. (2019). Oceanological and Hydrobiological Studies Non-indigenous tanaid *Sinelobus vanhaareni* Bamber, 2014 in the Polish coastal waters-an example of a successful invader. *Oceanological and Hydrobiological Studies, 45*, 121-130.

Christie, H., Norderhaug, K., & Fredriksen, S. (2009). Macrophytes as habitat for fauna. *Marine Ecology Progress Series*, *396*, 221–233.

Department of Ecology, Environment and Plant Sciences (2015). *Fucus radicans* – the Baltic Sea's newest species. Available from https://www.su.se/deep/english/about-us/news/fucus-radicans-the-baltic-sea-s-newest-species-1.249636. Accessed 2021-04-27.

Duffy, J. (2006). Biodiversity and the functioning of seagrass ecosystems. *Marine Ecology Progress Series*, *311*, 233–250.

Florin, A. B., & Lavados, G. (2010). Feeding habits of juvenile flatfish in relation to habitat characteristics in the Baltic Sea. *Estuarine, Coastal and Shelf Science*, *86*(4), 607–612.

Forslund, H., Eriksson, O., & Kautsky, L. (2012). Grazing and geographic range of the Baltic seaweed *Fucus radicans* (Phaeophyceae). *Marine Biology Research*, *8*(4), 322–330.

Gammal, J., Norkko, J., Pilditch, C. A., & Norkko, A. (2017). Coastal Hypoxia and the Importance of Benthic Macrofauna Communities for Ecosystem Functioning. *Estuaries and Coasts*, *40*(2), 457–468.

Gedan, K. B., & Bertness, M. D. (2010). How will warming affect the salt marsh foundation species *Spartina patens* and its ecological role? *Oecologia*, *164*, 479–487.

Google (n.d.). [Satellite view of the Baltic Sea]. Accessed 2020-11-20.

Google (n.d.). [Map of Askö area]. Accessed 2020-11-20.

Google (n.d.). [Map of Tvärminne area]. Accessed 2020-11-20.

Grabowski, J. H., Brumbaugh, R. D., Conrad, R. F., Keeler, A. G., Opaluch, J. J., Peterson, C. H., … Smyth, A. R. (2012). Economic Valuation of Ecosystem Services Provided by Oyster Reefs. *BioScience*, *62*(10), 900–909.

Häyren, E. (1949). Studier över vattnets vegetationoch flora i Stor-Pernåviken. *Bidrag Kännedom Finlands Natur Och Folk*, *93*(5), 1–62. (in Swedish)

HELCOM Red List Biotope Expert Group. 2013. Baltic photic mixed substrate, mud, coarse sediment or sand dominated by stable aggregations of unattached *Fucus* spp. (dwarf form).

HELCOM. (2018). Our Baltic Sea – State of the Baltic Sea – Second HELCOM holistic assessment.

Hubbel, S. (2001). The Unified Neutral Theory of Biodiversity and Biogeography.

Irigoyen, A. J., Trobbiani, G., Sgarlatta, M. P., & Raffo, M. P. (2011). Effects of the alien algae *Undaria pinnatifida* (Phaeophyceae, Laminariales) on the diversity and abundance of benthic macrofauna in Golfo Nuevo (Patagonia, Argentina): Potential implications for local food webs. *Biological Invasions*, *13*(7), 1521–1532.

Jacobson, P., Bergström, U., & Eklöf, J. (2019). Size-dependent diet composition and feeding of Eurasian perch (*Perca fluviatilis*) and northern pike (*Esox lucius*) in the Baltic Sea. *Boreal Environment Research 24*, 137-153.

Jakubavičiūtė, E., Bergström, U., Eklöf, J. S., Haenel, Q., & Bourlat, S. J. (2017). DNA metabarcoding reveals diverse diet of the three-spined stickleback in a coastal ecosystem. *PLOS ONE*, *12*(10), e0186929.

Karlson, K., Bonsdorff, E., & Rosenberg, R. (2007). The Impact of Benthic Macrofauna for Nutrient Fluxes from Baltic Sea Sediments. *AMBIO: A Journal of the Human Environment, 36(2)*, 161-167.

Kauppila, P., & Bäck, S. (2001). The state of Finnish coastal waters in the 1990s.

Kautsky, N., Kautsky, H., Kautsky, U., & Waern, M. (1986). Decreased depth penetration of Fucus vesiculosus (L.) since the 1940's indicates eutrophication of the Baltic Sea. *Marine Ecology Progress Series, 28*, 1-8.

Kersen, P., Kotta, J., Bučas, M., Kolesova, N., & Deķere, Z. (2011). Epiphytes and associated fauna on the brown alga *Fucus vesiculosus* in the Baltic and the North Seas in relation to different abiotic and biotic variables. *Marine Ecology*, *32*(SUPPL. 1), 87–95.

Kiirikki, M., & Blomster, J. (1996). Wind induced upwelling as a possible explanation for mass occurrences of epiphytic *Ectocarpus siliculosus* (Phaeophyta) in the northern Baltic Proper. *Marine Biology*, *127*(2), 353–358.

Kiirikki, M. (1996). Mechanisms affecting macroalgal zonation in the northern Baltic Sea. *European Journal of Phycology*, *31*(3), 225–232.

Korpinen, S., Jormalainen, V., & Pettay, E. (2010). Nutrient availability modifies species abundance and community structure of *Fucus*-associated littoral benthic fauna. *Marine Environmental Research*, *70*(3–4), 283–292.

Kotta, J., Vanhatalo, J., Jänes, H., Orav-Kotta, H., Rugiu, L., Jormalainen, V., … Johannesson, K. (2019). Integrating experimental and distribution data to predict future species patterns. *Scientific Reports*, *9*(1), 1–14.

Krumhansl, K. A., Okamoto, D. K., Rassweiler, A., Novak, M., Bolton, J. J., Cavanaugh, K. C., … Byrnes, J. E. K. (2016). Global patterns of kelp forest change over the past half-century. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(48), 13785–13790.

Leidenberger, S., Harding, K., & Jonsson, P. R. (2012). Ecology and Distribution of the Isopod Genus *Idotea* in the Baltic Sea: Key Species in a Changing Environment. *Journal of Crustacean Biology*, *32*(3), 359–389.

Leppäkoski, E., Olenin, S., & Gollasch, S. (2002). The Baltic Sea — A Field Laboratory for Invasion Biology. *Invasive Aquatic Species of Europe. Distribution, Impacts and Management* (pp. 253–259). Springer Netherlands.

Luther, H. (1981). Occurrence and ecological requirements of Fucus vesiculosus in semi-enclosed inlets of the Archipelago Sea, SW Finland. *Annales Botanici Fennici*, *18*(3), 187–200.

Meier, H. E. M. (2006). Baltic Sea climate in the late twenty-first century: a dynamical downscaling approach using two global models and two emission scenarios. *Climate Dynamics, 27*, 39-68.

Metzger, J. R., Konar, B., & Edwards, M. S. (2019). Assessing a macroalgal foundation species: community variation with shifting algal assemblages. *Marine Biology*, *166*(12), 156.

Meyer, J., Dahlke, S., Kafka, M., Kerkow, A., Lindner, C., Kube, S., … Blindow, I. (2019). Submerged vegetation in a shallow brackish lagoon does not enhance water clarity but offers substantial refuge for zooplankton. *Aquatic Botany*, *154*, 1–10.

Miller, R. J., Page, H. M., & Reed, D. C. (2015). Trophic versus structural effects of a marine foundation species, giant kelp (*Macrocystis pyrifera*). *Oecologia*, *179*(4), 1199–1209.

Nohrén, E., & Odelgård, E. (2010). Response of epibenthic faunal assemblages to varying vegetation structures and habitat patch size. *Aquatic Biology*, *9*(2), 139–148.

Olsen, J. L., Rouzé, P., Verhelst, B., Lin, Y. C., Bayer, T., Collen, J., … Van De Peer, Y. (2016). The genome of the seagrass *Zostera marina* reveals angiosperm adaptation to the sea. *Nature*, *530*(7590), 331–335.

Pandolfi, J. M., Bradbury, R. H., Sala, E., Hughes, T. P., Bjorndal, K. A., Cooke, R. G., … Jackson, J. B. C. (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science*, *301*(5635), 955–958.

Pereyra, R. T., Huenchuñir, C., Johansson, D., Forslund, H., Kautsky, L., Jonsson, P. R., & Johannesson, K. (2013). Parallel speciation or long-distance dispersal? Lessons from seaweeds (*Fucus*) in the Baltic Sea. *Journal of Evolutionary Biology*, *26*(8), 1727–1737.

R Core Team (2020). R: A language and environment for statistical computing (Version 4.0.3). R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Råberg, S., & Kautsky, L. (2008). Grazer identity is crucial for facilitating growth of the perennial brown alga *Fucus vesiculosus*. *Marine Ecology Progress Series*, *361*, 111–118.

Rodil, I. F., Attard, K. M., Norkko, J., Glud, R. N., & Norkko, A. (2020). Estimating Respiration Rates and Secondary Production of Macrobenthic Communities Across Coastal Habitats with Contrasting Structural Biodiversity. *Ecosystems*, *23*(3), 630–647.

Rohde, S., Hiebenthal, C., Wahl, M., Karez, R., & Bischof, K. (2008). Decreased depth distribution of *Fucus vesiculosus* (Phaeophyceae) in the Western Baltic: effects of light deficiency and epibionts on growth and photosynthesis. *European Journal of Phycology*, *43*(2), 143–150.

Roth, O., Kurtz, J., & Reusch, T. B. H. (2010). A summer heat wave decreases the immunocompetence of the mesograzer, *Idotea baltica*. *Marine Biology*, *157*(7), 1605–1611.

Rumohr, H., Brey, T., & Ankar, S. (1987). A Compilation of Biometric Conversion Factors for Benthic Invertebrates of the Baltic Sea.

Ruuskanen, A., & Bäck, S. (1999). Morphological variation of northern baltic sea fucus vesiculosus l. *Ophelia*, *50*(1), 43–59.

Svedelius, N. (1901). Studier öfver Östersjöns hafsalgsflora. PhD thesis. University of Uppsala. (in Swedish)

Szaniawska, A. (2018). Baltic Crustaceans.

Takolander, A. (2018). Assessing the effects of climate change on Baltic Sea macroalgae : implications for the foundation species *Fucus vesiculosus* L. PhD thesis. University of Helsinki.

Takolander, A., Cabeza, M., & Leskinen, E. (2017a). Climate change can cause complex responses in Baltic Sea macroalgae: A systematic review. *Journal of Sea Research, 123*, 16-29.

Takolander, A., Leskinen, E., & Cabeza, M. (2017b). Synergistic effects of extreme temperature and low salinity on foundational macroalga *Fucus vesiculosus* in the northern Baltic Sea. *Journal of Experimental Marine Biology and Ecology*, *495*, 110–118.

Tatarenkov, A., Bergström, L., Jönsson, R. B., Serrão, E. A., Kautsky, L., & Johannesson, K. (2005). Intriguing asexual life in marginal populations of the brown seaweed *Fucus vesiculosus*. *Molecular Ecology*, *14*(2), 647–651.

Tiblom, O. (2017). The associated flora and fauna of free-living *Fucus vesiculosus* in the Baltic Sea. Master's thesis. University of Stockholm.

Tolvanen, H., Suominen, T., & Kalliola, R. (2013). Annual and long-term water transparency variations and the consequent seafloor illumination dynamics in the Baltic sea archipelago coast of SW Finland. *Boreal Environment Research*, *18*, 446–458.

Torn, K., Krause-Jensen, D., & Martin, G. (2006). Present and past depth distribution of bladderwrack (*Fucus vesiculosus*) in the Baltic Sea. *Aquatic Botany*, *84*(1), 53–62.

Torres, A. C., Veiga, P., Rubal, M., & Sousa-Pinto, I. (2015). The role of annual macroalgal morphology in driving its epifaunal assemblages. *Journal of Experimental Marine Biology and Ecology*, *464*, 96–106.

Vásquez, J. A., Zuñiga, S., Tala, F., Piaget, N., Rodríguez, D. C., & Vega, J. M. A. (2014). Economic valuation of kelp forests in northern Chile: values of goods and services of the ecosystem. *Journal of Applied Phycology*, *26*(2), 1081–1088.

Wikström, S. A., & Kautsky, L. (2007). Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. *Estuarine, Coastal and Shelf Science*, *72*(1–2), 168–176.

Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J., & Graham, N. A. J. (2019). Coral reef ecosystem services in the Anthropocene. *Functional Ecology*, *33*(6), 1023–1034.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., … Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, *314*(5800), 787–790.

WoRMS Editorial Board (2021). World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2021-04-22.

8. Supplementary material

Table S1. Biomass of applicable epifaunal taxa of free-living *Fucus vesiculosus* (dry weight g m^{-2}).

	Askö			*TZS*		
Taxa	A1	A2	A3	T1	T2	T3
CRUSTACEA						
Asellus aquaticus				1,7411	0,0667	
Gammarus spp.	0,337711	0,175933	0,266933	1,524756	1,215356	4,780533
Idotea balthica						0,192267
Idotea chelipes		0,138756	0,166011			
Idotea sp.			0,106544			
Jaera albifrons						0,004433
INSECTA						
Chironomidae spp.	1,765833	0,086667	0,043333	0,101833	0,002167	0,4875
Trichoptera spp.	0,7172			0,3608	2,684	2,8908
MOLLUSCA						
Bithynia sp.	0,012895			0,793432	0,843156	0,051717
Cerastoderma glaucum				22,04037		1,95612
Peringia spp.	36,99746	45,14816	29,72753	10,20675	1,450029	5,497651
Limecola balthica			2,816226	3,884222	0,029255	0,934513
Mytilus edulis	111,2515	4,567078	48,02947	2,757187	0,97306	0,016189
Parvicardium hauniense	14,96677	17,84936	20,61724	8,7438	0,3802	
Potamopyrgus antipodarium			0,724638	1,470723		2,944661
Radix sp.	0,696197			0,170398	0,86382	1,881598
Theodoxus fluciatilis	15,95173	39,77879	21,91673	51,82694	74,35155	27,30789
NEMERTEA						
Cyanopthalma obscura	0,100222		0,002278			
ANNELIDA						
Hediste diversicolor	0,085478		0,0628			
Oligochaeta spp.	0,044333	0,061222	0,092889	0,016889		
SUM	183	108	125	106	83	49

Table S2. Biomass of applicable infaunal taxa of free-living *Fucus vesiculosus* (dry weight g m^{-2}).

	Askö			*TZS*		
Taxa	A1S	A2S	A3S	T1S	T2S	T3S
CRUSTACEA						
Gammarus sp.					3,842459	
INSECTA						
Chironomidae spp.				4,354435	2,295975	0,554201
MOLLUSCA						
Bithynia sp.				1,430659	3,602271	
Peringia spp.	18,2327	8,607106	21,59045	3,554791	28,70102	14,96075
Limecola balthica	180,9525	63,37349	12,73355	55,37267	101,5836	512,243
Mytilus edulis	4,385279					
Parvicardium hauniense				38,59531		
Potamopyrgus antipodarium					3,665378	
Theodoxus fluviatilis			14,10858	30,82126		
ANNELIDA						
Hediste diversicolor	45,64016	2,54973	29,06692			9,306514
Oligochaeta spp.	1,079981	2,159962	0,385708	0,308566		
SUM	249	76	66	79	210	541

Table S3. Biomass of applicable (Control) infaunal taxa of bare sediment (dry weight g m^{-2}).

	Askö			*TZS*		
Taxa	A1C	A2C	A3C	T1C	T2C	T3C
INSECTA						
Chironomidae spp.	0,475029	0,395858		1,266745	21,53466	
MOLLUSCA						
Cerastoderma glaucum		248,1033				
Peringia spp.	183,9058	66,08097	17,27863	5,776044		
Limecola balthica	146,7274	41,63942	41,13496	1173,557	200,742	119,0795
Mytilus edulis	79,01751					
Parvicardium hauniense	84,45867	102,4326				
Potamopyrgus antipodarium			3,874141			
NEMERTEA						
Cyanopthalma obscura				0,083232		
ANNELIDA						
Bylgides sarsi						0,062119
Hediste diversicolor	23,26629		80,82644			
Oligochaeta spp.	0,617132		1,697113	5,399906		
SUM	518	459	141	1190	222	119